JOURNAL
OF THE
ARNOLD ARBORETUM

VOLUME 71 OCTOBER 1990 NUMBER 4

THE GENERA OF CARDUEAE (COMPOSITAE; ASTERACEAE) IN THE SOUTHEASTERN UNITED STATES[1]

RANDALL W. SCOTT[2]

Tribe **Cardueae** Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88:** 155. 1819, "Carduineae."

Perennial to annual herbs [rarely shrubby or tree-like]. Leaves alternate, sinuate, lobed, pinnatifid or pinnatisect, rarely entire, commonly spiny margined. Capitula (heads) homogamous or heterogamous with carpellate or neuter (sterile) and partly radiating marginal flowers. Involucral bracts ovate to lanceolate [bristles], imbricate in several series, often with an apical spine, bristle, or membranaceous appendage. Receptacle setaceous, bristly, hairy or honeycombed [naked or with connate bracts partially split at the upper margin].

---

[1] Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and at this writing supported by BSR-8415769 (Carroll E. Wood, Jr., principal investigator), under which this account was prepared, and BSR-8415637 (Norton G. Miller, principal investigator). This treatment, the 134th in the series, follows the format established in the first paper (Jour. Arnold Arb. **39:** 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family, subfamily, tribe, subtribe, or genus in brackets [ ]. Those references that I have not verified are marked with an asterisk.

I want to thank Carroll Wood for his extensive and constructive comments, both editorial and otherwise. Particular thanks go to Tina Ayers without whose support this project might never have been completed. Ihsan Al-Shehbaz and Barbara Callahan were very helpful with bibliographic searches, while I was at Harvard. For assistance manifested in a variety of ways, I want to thank David Boufford, Barbara Nimblett, Cathy Paris, John Pruski, Stephen Spongberg, and Emily Wood.

The illustration was drawn under an earlier NSF grant by Rachel A. Wheeler supervised by George K. Brizicky from materials collected by C. E. Wood, Jr. (a–e, j) and J. K. Small (*8122*, GH) in Florida, and by R. B. Channell and H. F. L. Rock in southeastern North Carolina.

[2] Arnold Arboretum of Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138. Present address: Department of Biological Sciences, Northern Arizona University, P. O. Box 5640, Flagstaff, Arizona 86011.

Journal of the Arnold Arboretum **71:** 391–451. October, 1990.

Pappus of simple or plumose bristles or paleaceous, uniseriate (*Echinops*) or multiseriate, free or basally fused, of nearly equal length (Carduinae), or the inner longer (Centaureinae). Corollas tubular (*Echinops*), actinomorphic, divided into tube and limb, the outer florets occasionally zygomorphic (falsely radiate) (*Cirsium, Centaurea*), lobes narrow or linear [triangular] and, in many cases, elongated. Anthers with sagittate basal appendages, these entire or denticulate [laciniate]; filaments hairy, papillose or glabrous; pollen variable, but basic type spherical, spiny, tricolporate (see Wagenitz, 1955; Štepa). Styles very long, united and only diverging at the tips (see Solbrig, 1963, *fig. 2, l*) or widely divergent or very short and divergent, often with a distinct collar of hairs at or below the base of the flat, elliptical or semi-cylindrical, acute to acuminate, often papillose branches, the stigmatic papillae on the inner surface. Achenes mostly obovate, elongate-conoidal or fusiform, commonly somewhat bossed on the upper, abaxial side, occasionally laterally compressed, glabrous or sparsely covered with one-celled hairs or shortly forked twin hairs to densely villous (*Echinops*); often with a distinctly marked apical crown or margin; detachment area of achenes straight and basal (*Echinops*), straight and lateral-adaxially, lateral-abaxially, rarely basally oriented (Carduinae) or concave and lateral-adaxially oriented (Centaureinae); seed often with a basal or lateral (*Centaurea* and related genera) hilum. (Carlineae Cass., Jour. Phys. **88:** 152. 1819; Centaurieae Cass., *Ibid.* 154; Echinopseae Cass., *Ibid.* 157; Cynareae Less., Linnaea **5:** 128. 1830, nom. illegit. [includes *Carduus* L., type of Cardueae Cass.].) TYPE GENUS: *Carduus* L.

Nearly 80 genera (ca. 2500 spp.; Dittrich, 1977) traditionally placed in four subtribes, but more recently (Dittrich, 1977) segregated into three tribes: Echinopseae Cass., Carlineae Cass., Cardueae Cass., with the last divided into subtribes Carduinae Dumort. and Centaureinae Dumort. Genera known from the Southeast belong to the Cardueae (Dittrich, 1977). *Arctium* L., *Carduus* L., *Cirsium* Miller, *Onopordum* L., and *Silybum* Adanson were placed in the Carduinae and *Centaurea* L. and *Cnicus* L. in the Centaureinae. The Echinopseae Cass. may be represented in the Southeast by *Echinops* L., but there is no solid evidence that any of the cultivated species has escaped from cultivation there. Centers of diversity are in Europe and western Asia. About 35 species in eight genera occur in the southeastern United States. The great majority of the North American representatives of this tribe have been introduced from Europe. Native taxa from the Southeast occur only in *Cirsium* (all but two of the nearly fifteen species are indigenous) and *Centaurea* (one of eight species is native).

Considerable diversity of opinion has been expressed in the nomenclatural history of the Cardueae. In a serial treatment that extended over a period of nearly fifteen years, Cassini (1816–1830) described numerous taxa in the tribes Cardueae Cass., Centaurieae Cass., Carlineae Cass., and Echinopseae Cass. These tribes were first described under their French names (Cassini, 1817), but were later given Latin names by Cassini (1819). Two years after Cassini finished his serial treatment, Lessing presented a more inclusive treatment of the family wherein he placed most of six of Cassini's tribes under the illegitimate name Cynareae Less. Bentham (1873a, b) included four of Cassini's tribes in the

Cardueae ["Cynaroideae"] in what came to be the traditionally accepted view of the tribe. Most recently, Dittrich (1977) recognized three tribes in lieu of Bentham's single broadly circumscribed one.

As indicated by Dittrich (1977), the superfluous name Cynareae, coined by Lessing, has been used by many authors (e.g., Boissier; Bentham; Hoffmann) and still persists in contemporary works (e.g., Carlquist, 1965; Cronquist, 1955, 1977; Dittrich *et al.,* 1979, 1980; Clapham *et al.*; Jeffrey, 1968; Johnson 1974, 1975).

The following genera known from the southeastern United States were included in Cassini's Cardueae: *Arctium* (as *Lappa* Scop.), *Carduus, Cirsium, Onopordum,* and *Silybum.* He placed *Cnicus* and *Centaurea* in the Centaurieae. Several taxa treated by Cassini as subtribe Xeranthemées of the tribe Carlineae have been placed in the Cardueae by subsequent workers.

In a treatment published a year before Cassini finished his extended serial treatment of the Compositae, Dumortier retained the tribes Echinopseae (as Echinopsideae) and Cardueae (as Carduaceae), but reduced Cassini's tribes Carlineae and Centaurieae to subtribes of the Cardueae.

Lessing incorporated all or parts of five of Cassini's tribes (Arctotideae, Calenduleae, Cardueae, Centaurieae, Echinopseae) and the subtribe Xerantheminae Cass. as subtribes of the tribe Cynareae. Many members of Cassini's tribe Carlineae were treated under the subtribe Carduinae, while two new subtribes, Cardopateae Less. and the Othonninae Less., were proposed for other representatives of this group.

With few exceptions, A. P. de Candolle, among others, accepted Lessing's broad view of the Cardueae. De Candolle reduced subtribe Othonninae to a division of the Calenduleae, elevated three of Lessing's divisions (Carlineae, Serratuleae, Silybeae) to subtribal status and extracted a twelfth subtribe (Carthaminae) from Lessing's subtribe Centaurieae.

As treated by Bentham (1873a), the Cardueae ("Cynaroideae") contained nearly 36 genera in the four subtribes Carduineae, Carlineae, Centaurieae, and Echinopsideae. Lessing's subtribes Cardopatiinae and Xerantheminae (sensu De Candolle) were incorporated into the subtribe Carlineae, while De Candolle's subtribes Carthaminae and Silybinae were included in the Centaurieae and Carduineae, respectively. Similarly, the subtribe Serratulinae (Less.) DC. was divided between the Carduineae and Centaurieae. Cassini's tribes Arctotideae and Calenduleae were resurrected from the subtribal status accorded them by Lessing and De Candolle.

Cassini's system was considered to be a "natural" one by Dittrich (1977), who divided the Cardueae into tribes Echinopeae [sic] (2 genera), Carlineae (11 genera), and Cardueae (66 genera). These he grouped together under the subfamily name Cynaroideae, a name used by Bentham at the tribal level, but without any prior usage at the subfamilial level known to the present author. Dittrich noted that no single character unites the three tribes as he delimited them, not even the traditional stylar character, which he found to be limited to the Cardueae *sensu stricto,* and that between these three groups no connecting forms are known. The Echinopseae are distinguished by their globose, secondary heads comprised of numerous uniflorous heads and by their corollas with long, slender lobes. The Carlineae have capitula with numerous florets, characteristically short corolla lobes, and receptacles with connate paleae. The Cardueae have long, slender corolla lobes, bristly receptacles, flat and elliptical style branches (in contrast to the half-cylindric or cylindric, usually acuminate branches of the other two tribes), papillose to hairy anther filaments, and laterally compressed achenes. Dittrich further divided the Cardueae into the Carduinae and Centaureinae on the basis of characteristics of the pappus (bristles of almost equal length and form vs. bristles or scales elongated from outside to inside; the internal pappus elements often morphologically different from the outer, forming a "double pappus") and the detachment areas of the achenes (straight, lateral-adaxially, rarely basally oriented vs. always concave and of lateral-adaxial orientation). Whereas Bentham recognized 10 genera of the subtribe Centaureinae, Dittrich (1977) recognized 27, many of which are segregates from *Centaurea.*

In a chemical review of the Cardueae *sensu lato,* H. Wagner (1977) preferred to view the group as comprising two tribes, the Carlineae and the Cardueae. The Echinopseae are apparently treated as a subtribe of the Carlineae, while the Cardueae are divided into two subtribes, the Carduinae and the Centaureinae. The taxa of both tribes are inclusively referred to as the Cynareae throughout his paper.

As delimited by Bentham (1873a), the Cardueae comprise the largest tribe of Compositae in the North Temperate region of the Old World. Bentham thought that the tribes with the closest connections to the Cardueae (Cynareae) were the principally South American Mutisieae (subtribe Gochnatinae) and the South African Arctotideae (subtribe Gorterinae). The latter tribe he considered to be a possible link between the northern tribes Cardueae and Anthemideae.

On the basis of seed anatomy, Lavialle linked the Cardueae (Cynarées) to the Mutisieae (Mutisées) through *Xeranthemum* L. Cronquist (1955, 1977) reaffirmed the close relationship between Mutisieae, Vernonieae, Arctotideae, and Cardueae, but disagreed with Carlquist (1961, 1976), who grouped them with the Lactuceae in subfamily Cichorioideae. While the close relationship of the Arctotideae and Cardueae is not disputed, the position of the Arctotideae was considered problematic by Cronquist (1955, 1977), since he considered them a bridge between the radiate and discoid tribes.

Carlquist (1976) proposed two subfamilies for the Compositae (Asteraceae) and aligned the Cardueae with tribes Arctoteae, Lactuceae ("Cichorieae"), Eupatorieae, Vernonieae and Mutisieae in the subfamily Cichorioideae ("the mutisioid line" vs. the subfamily Asteroideae or "helianthoid line"). Both Carlquist (1976) and Jeffrey (1977) have suggested that the ligulate flowers of the Cichorioideae are modified bilabiate flowers distinctly different and of a separate origin from the ray flowers found in the Asteroideae. Carlquist considered the expanded flowers found in the Arctoteae and Cichorioideae to have originated in the same manner and included the Arctoteae in this subfamily. Cronquist (1977) disputed Carlquist's conclusions about the Arctotideae on the grounds that the external morphology of the ray flowers found in many representatives of the Arctoteae is much like that of the Asteroideae and that Carlquist rested his opinions concerning the alignment of the Arctoteae on

Didelta tomentosum Less., the ray flowers of which have three, four, or five teeth. Carlquist (1976) thought that the Cardueae originated in the Old World (Northern Hemisphere) and that the Arctoteae are the result of "explosive evolution of a stock related to a cichoriead-carduaead complex in southern Africa." While warning that wood anatomy is not a particularly good character on which to establish tribal relationships, Carlquist (1965) noted that the wood anatomy of the Cardueae would not contradict Bentham's (1873b) proposed relationships between the tribes Carduеae, Mutisieae, and Vernonieae.

Jeffrey (1978) recognized 17 tribes and the two subfamiles Lactucoideae (correctly, Cichorioideae Kitamura) and Asteroideae in his treatment of the Asteraceae. He placed the tribes Cardueae and Arctoteae in subfamily Lactucoideae, along with tribes Lactuceae, Arctoteae, Eremothamneae (a monotypic tribe from South Africa), Vernonieae, Liabeae, and Eupatorieae. The Cardueae were said by Jeffrey to have three subtribes that we may presume to be Carduinae, Centaureinae, and Echinopsinae, since he did not follow Dittrich's recognition of the Echinopseae at the tribal level.

In a study of particular interest, Bremmer tacitly supported Dittrich's division of the Cardueae into three tribes. Bremmer contended that the phylogenetic relationships between the Arctoteae and Dittrich's three tribes are unclear and that the Echinopseae, Carlineae, and Cardueae are conceivably monophyletic taxa. If Dittrich's three tribes are treated as a single tribe from which the Arctoteae are excluded, Bremmer claimed that the Cardueae *sensu lato* may not represent a monophyletic group. This is illustrated in the cladogram presented by Bremmer in which the four groups are shown as independent lineages arising from a common ancestor. The Cardueae *sensu stricto* were characterized by three unique characters: 1) papillose to hairy anther filaments, 2) testa epidermal cells in a lignified palisade layer, becoming hard and dark brown to black, and 3) nuclear endosperm. The Echinopseae were distinguished by their secondary heads composed of numerous uniflorous heads and by echinopsine alkaloids, but they were noted as lacking the lactiferous tissue typical of other members of the subfamily Cichorioideae. Neither the Carlineae nor the Arctotideae are delimited by unique characters. The Carlineae are set off as having paleaceous receptacles and shortly lobed disc corollas, while the Arctotideae are said to have true apically three-lobed ray florets and to lack the caudate anthers found in the other three tribes.

Haslett *et al.* and Boulter *et al.* used the analysis of plastocyanin amino acids extracted from species representing eight tribes of the Compositae in a phylogenetic study of the family. Their data support the view that the Compositae are a natural group and indicate a close relationship between the Lactuceae and Cardueae. Indicative of the Cardueae's possibly primitive position among the Compositae was the basal position occupied by *Centaurea* in the phylogeny generated from the data of Boulter *et al.* Bremmer noted that the Cardueae and Lactuceae are the only "cichorioid" tribes included in these studies and that the positions of *Senecio* L. and *Taraxacum* Wigg. indicate a lack of sufficient data from which to draw an unequivocal conclusion.

Support for the primitive position of the Cardueae can be inferred from Bolick's studies on the pollen of Compositae. Bolick described two basic pollen types in the Compositae: a caveate Helianthoid pattern and a non-caveate Anthemidoid pattern, which Bolick claimed to be less specialized in its structure than the Helianthoid type. The Cardueae were found to have Anthemidoid-type pollen similar to that of the Mutisieae and Vernonieae. Helianthoid pollen is characteristic of the remaining tribes, except for the Anthemideae, Arctoteae, and Lactueae, tribes in which both types of pollen were found.

Recent analyses of chloroplast DNA (Jansen & Palmer) support the hypothesis that the Mutisieae (subtribe Barnadesiinae), not the Cardueae, may be the most primitive subtribe of the family, since members of this tribe lack in their chloroplast genome an inversion characteristic of the other members of the family. The phylogenetic interpretations of Jansen & Palmer have been questioned by Robinson, who showed, in figure form, a hypothetical phylogeny based on Jansen & Palmer's proposal that closely aligned the Cardueae with the Mutisieae (save for the subtribe Barnadesiinae).

Wagner characterized the chemistry of the group as being for the most part similar to the rest of the family. He reported volatile and non-volatile terpenoids, acetylenes, phenolic compounds, and especially hydroxycinnamic acid derivatives and flavonoids as characteristic compounds of the tribe. In addition to a variety of common monoterpenes and triterpenoids of the beta-oleanane and lupane type, Wagner noted that sesquiterpene lactones of the germacrane type are characteristic of the Carduinae and Centaureinae. Further discussion of the structural similarities of these compounds can be found in Hermout & Šorm, who noted that the germacranolides isolated from the Cardueae are strikingly uniform in their structure. The guaianolides cynaropicrin and costuslactone have been found in *Cynara* L. and *Saussurea* DC., while elemanolides have been found in *Centaurea* species. Seaman suggested that the presence of certain C-6 *trans*-lactonized guaianolides and germacrolides and occasionally elemanolides found in 11 genera of the Cardueae may be useful in determining tribal limits. Wagner (1977) noted that the subtribe Centaureinae seemed to be the best differentiated in that in this group are found nearly all types of acetylenes found in the Cynaroideae, a variety of highly methoxylated flavonoids (including flavanones and lignans) and sesquiterpenoids. Whereas the Carduinae contain special acetylenes (e.g., C_{17} acetylenes, acetylene glycosides), sesquiterpenoids of the guaianolide type, monomethoxylated flavonoids, and simple cinnamic acids and derivatives, the Centaureinae have acetylene aldehydes, acetylene chlorohydrins and acetates, sesquiterpene lactones of the germacranolide type, highly methoxylated flavonoids, and typical fully methoxylated lignans. Nowak and coworkers have indicated that cynaropicrin may prove to be a chemical marker for subtribe Centaureinae.

Acetylenes appear to be well differentiated among the subtribes of the Cardueae (Bohlmann *et al.*). Thiophenes in considerable variety were said to be typical of *Echinops* and *Xeranthemum*, furan derivatives were found among members of the Carlininae (*Carlina* L., *Atractylis* L.), and ene-tetrayenes are common constituents in members of the Carduinae (*Arctium, Carduus, Cirsium, Silybum, Onopordum*). While the Centaureinae are not well differentiated chemically from the other subtribes, they do have unique chlorohydrines and -acetates (*Centaurea, Carthamus* L.) not found in the other subtribes, as well as unsaturated aldehydes in the aerial parts and ene-tetrayene-ene in the roots.

Flavonoids occur predominantly as flavones and flavonols (flavanones and flavanonols are restricted to *Carthamus, Centaurea* and *Silybum*). *Silybum* is unique in the tribe in that it produces flavonolignans. Highly methoxylated flavonols and flavones are commonly found in *Centaurea* and *Cirsium*. Wagner further reported that flavonoids are normally found in the glycosidic form with 3-O-glycosides and 4′-O-glycosides as the most common forms.

Other phenolic compounds reported by Wagner for the Centaureinae and Carduinae are cinnamic acids and their derivatives. Tannins are generally absent or occur sporadically. Species of *Arctium, Carthamus,* and *Centaurea* have the dimeric phenylpropane derivatives arctiin and hydroxyarctiin. These compounds were reported to be of physiological importance in the seeds of these taxa and were thought to be restricted to the Carduinae and Centaureinae (Wagner).

Alkaloids are widespread in the Cardueae, but the structures of only a few have been elucidated (Wagner). Amines and cyanogens appear to occur sporadically with only tyramine and histamine reported from *Silybum* and choline from *Onopordum, Saussurea,* and *Centaurea* (Wagner).

Moore & Frankton (1962) proposed a base chromosome number of 17 for the tribe. They suggested that lower numbers have been derived through reduction brought about by translocations with a possible loss of non-essential chromatin and inactivation of excess centromeres. They further noted that this process has occurred in many genera and may have contributed to speciation. They thought that genera with the same chromosome number are not necessarily closely related, nor are those with different chromosome numbers distantly related, since different chromosome numbers do not prevent ready hybridization between taxa. They stressed the importance of evaluating both chromosome morphology and chromosome number when assessing generic relationships.

Achene characters have proved to be the most reliable ones in the delimitation of genera within the Cardueae and have been the subject of several in-depth studies (Dittrich, 1968a & b, 1970; Isley; Lavialle; Singh & Pandey). The four subtribes of the Cardueae are readily distinguished on the basis of their achenes. According to Lavialle and Dittrich, achene characters clearly segregate the Echinopsinae and Carlininae from the closely aligned Carduinae and Centaureinae. Pappus characters and those of the apical region of the achene allowed Dittrich (1970) to distinguish three groups of genera within the Carduinae: 1) *Cirsium, Carduus,* and *Silybum,* 2) *Cynara, Notobasis* Cass., *Ptilostemon* Cass., *Arctium,* and *Onopordum,* 3) *Galactites* Moench, *Picnomon* Adanson, *Tyrimnus* Cass., and *Jurinea* Cass. Dittrich's study (1968a & b) of the Centaureinae informally grouped taxa of this subtribe on the basis of whether the hilum was basal (e.g., *Serratula* L., *Rhaponticum* Hill, *Leuzea* DC.), lateral (*Carduncellus* Adanson, *Carthamus,* sections of *Centaurea*), or caudate (*Cnicus,* sections of *Centaurea*).

The Cardueae have economic significance in several areas, perhaps, most notably, as a source of noxious weeds that have overgrown much agricultural land throughout the world. Species of *Centaurea, Cirsium, Echinops,* and other genera of the tribe are cultivated as ornamentals. *Cynara Cardunculus* L., the cardoon, has long been cultivated for the petioles of its leaves that are eaten like celery. The bracts and the receptacle of immature heads of *C. Scolymus* L., which is probably derived from *C. Cardunculus,* are commonly eaten as the globe artichoke. Species of *Centaurea* have been noted as important sources of nectar for honey bees (Goltz).

Echinops, a genus of about 120 species (Mabberley) distributed in southern Europe, North Africa, temperate and subtropical Asia, northward to Japan, and naturalized in parts of North America, has been included by Cronquist (1980) as a member of the flora of the southeastern United States. Three species of the genus (*E. sphaerocephalus* L., *E. exaltatus* Schrader, and *E. bannaticus* Rochel ex Schrader) are often grown as ornamentals (*E. bannaticus* frequently as *E. Ritro* L.; see Karlsson). Cronquist (1980) noted that *E. sphaerocephalus* has escaped from cultivation and become casually established in parts of the United States and southern Canada. *Echinops sphaerocephalus* is the only species of *Echinops* treated in floras of the northeastern United States (e.g., Fernald; Gleason & Cronquist), but it has not been included in any of the floras for the Southeast (e.g., Chapman; Long & Lakela; Radford *et al.*; Rickett; Small, 1933, among others), nor have I seen specimens that would indicate that *E. sphaerocephalus* has become established in the Southeast. Since the three species mentioned above are commonly cultivated, it is reasonable to expect that one or more of them may eventually become established in some areas of the Southeast. *Echinops* is included here in brackets in the key to genera, and various selected references are among those that follow.

REFERENCES:

ARANO, H. The karyotype analysis and its karyotaxonomic considerations in some genera of subtribe Carduinae. Jap. Jour. Genetics **32:** 323–332. 1957.

BARKLEY, T. M. A manual of the flowering plants of Kansas. 402 pp. Kansas State University Endowment Association, Manhattan, Kansas. 1968. [Key to Cynareae, 373; *Arctium, Cirsium, Carduus, Onopordum, Carthamus, Centaurea,* 374–376. See also GREAT PLAINS FLORA ASSOCIATION.]

BENTHAM, G. Compositae. *In:* G. BENTHAM & J. D. HOOKER. Gen. Pl. **2:** 163–533. 1873a.

———. Notes on the classification, history, and geographical distribution of Compositae. Jour. Linn. Soc. Bot. **13:** 335–582. 1873b.

BOBROV, E. G., & S. K. CZEREPANOV, eds. Cynareae. (In Russian.) Fl. URSS (SSSR). **28.** xx + 655 pp. Moscow, Leningrad. 1963. [Thirty-nine genera by 13 authors. Only genera pertinent to the southeastern United States are cited here: *Carduus,* 4–39, by S. G. TAMAMSHIAN; *Cirsium,* 51–125, 111 species, by A. L. KHARADZE; *Cynara,* 225, 226, by S. G. TAMAMSHIAN; *Silybum,* 227, 228, by S. G. TAMAMSHIAN; *Onopordum,* 228–240, by S. G. TAMAMSHIAN; *Centaurea,* 370–578, 178 species, 22 subgenera by M. V. KLOKOV, D. I. SOSNOVSKY, N. N. TSVELEV, & S. K. CZEREPANOV; *Carthamus,* 581–587, by S. A. SHOSTAKOVSKY; *Cnicus,* 587, 588, by M. M. ILJIN; *Echinops,* **27:** 1–53. 1962, by E. G. BOBROV.]

BOHLMANN, F., T. BURKHARDT, & C. ZDERO. Naturally occurring acetylenes. 547 pp. London & New York. 1973. [Various taxa and their constituents listed, 442–461; *Arctium,* 445; *Carduus,* 447; *Cirsium,* 447, 448.]

BOISSIER, E. Flora orientalis. Vol. 3. 1033 pp. Geneva. 1875. [Subtribe Carduinae, 457–711; *Arctium* (as *Lappa* Tourn.) 4 spp., 457, 458; *Cirsium,* 74 spp., 523–553; *Silybum,* 1 sp., 556; *Centaurea,* 183 spp., 614–695; *Cnicus,* 1 sp., 705, 706.]

BOLICK, M. R. Taxonomic, evolutionary and functional considerations of Compositae pollen ultrastructure and sculpture. Pl. Syst. Evol. **130:** 209–218. 1978.

BORNMÜLLER, J. Revisionsergebnisse einiger orientalischer und zentralasiatischer Arten der Gattung *Echinops*. Beih. Bot. Centralbl. **36:** 200–228. 1918. [Section *Oligolepis* revised and new sect. *Pleiacme* and ten new species described.]

BOULTER, D., J. T. GLEAVES, B. G. HASLETT, D. PEACOCK, & U. JENSEN. The relationships of 8 tribes of the Compositae as suggested by plastocyanin amino acid sequence data. Phytochemistry **17:** 1585–1589. 1978.

BREMMER, K. Tribal interrelationships of the Asteraceae. Cladistics **3:** 210–253. 1987.

BRIQUET, J. *In:* E. BURNAT, J. BRIQUET, & F. CAVILLIER. Composées Cynaroïdées. Flore des Alpes Maritimes. Vol. 7. 311 pp. Genève. 1931. [*Cirsium*, 13 spp., 11–55; *Carduus*, 9 spp., 55–94; *Centaurea* 17 spp., 94–215; *Arctium*, 4 spp., 264–278.]

BRIZICKY, G. K. Subgeneric and sectional names: their starting points and early sources. Taxon **18:** 643–660. 1969.

BUNGE, A. VON. Über die Gattung *Echinops*. Bull. Acad. Sci. St. Pétersbourg **6:** 390–411. 1846.

BURTT, B. L. Compositae and the study of functional evolution. Trans. Proc. Bot. Soc. Edinburgh **39:** 216–232. 1961.

CANDOLLE, A. P. DE. Cynareae. Prodr. Syst. Nat. **6:** 449–678. 1837. [*Centaurea* 565–605; *Cnicus* 606–609; *Silybum* 616; *Carduus* 621–633; *Cirsium* 634–657; *Arctium* (as *Lappa* Tourn.) 661–662.]

CARLQUIST, S. Comparative plant anatomy. New York. 146 pp. 1961.

———. Wood anatomy of Cynareae (Compositae). Aliso **6:** 13–24. 1965.

———. Tribal interrelationships and phylogeny of the Asteraceae. Aliso **8:** 395–492. 1976.

CASSINI, H. Compositae. *In:* G. CUVIER, ed., Dictionnaire des sciences naturelles **1-60.** ed. 2. Paris. 1816–1830. [A description of the tribe "Carduacées" appears in vol. 7, p. 94; "Centauriées" in vol. 7, p. 376; "Echinopsées" in vol. 14, p. 200. A summation appeared in vol. 60, p. 568. See also, KING, R. M., & H. D. DAWSON. Cassini on Compositae. Oriole editions, New York. 1975. 3 vols. A valuable facsimile compilation of Cassini's works collected from the original Dictionnaire articles.]

———. Sixième mémoire sur l'ordre des Synanthérées, contenant les caractères des tribus. Jour. Phys. Chim. Hist. Nat. Arts **88:** 150–163. 1819. [In this article, Cassini gave both Latin names and descriptions for his tribes previously described in French; see citation above for Cassini 1816–1830.]

———. Sixième mémoire sur l'ordre des Synanthérées. *In:* Opuscules phytologiques. Vol. 1. lxvii + 426 pp. Paris. 1826.

CHAPMAN, A. W. Flora of the southern United States. ed. 3. xxxix + 641 pp. Cambridge, Massachusetts. 1897. [Cynareae, 268, 269.]

CLAPHAM, A. R., T. G. TUTIN, & D. M. MOORE. Flora of the British Isles. ed. 3. xxix + 688 pp. Cambridge, England. 1987. [*Echinops, Carlina, Arctium, Carduus, Cirsium, Silybum, Onopordum, Cnicus, Centaurea,* 479–490.]

CORRELL, D. S., & M. C. JOHNSTON. Manual of the vascular plants of Texas. xv + 1881 pp. Renner, Texas. 1970. [*Centaurea, Cirsium, Carduus, Silybum, Carthamus, Onopordum,* 1713–1720.]

CRONQUIST, C. Phylogeny and taxonomy of the Compositae. Am. Midl. Nat. **53:** 478–511. 1955.

———. The Compositae revisited. Brittonia **29:** 137–153. 1977.

———. Asteraceae. Vascular flora of the southeastern United States. Vol. 1. xv + 261 pp. Chapel Hill, North Carolina. 1980. [Key to Cynareae, 11, 12; *Arctium, Carduus, Cirsium, Silybum, Onopordum, Echinops, Centaurea, Cnicus,* 218–228.]

———. An integrated system of classification of flowering plants. xxviii + 1262 pp. New York. 1981. [Order Asterales, 1020–1028.]

———. History of generic concepts in the Compositae. Taxon **34:** 6–10. 1985.

DAVIS, P. H., & A. J. C. GRIERSON, eds. Compositae. *In:* P. H. DAVIS, ed., Flora of Turkey. Vol. 5. 890 pp. Edinburgh. 1975. [*Arctium, Cnicus* by F. K. KUPICHA; *Cynara, Silybum* by F. K. KUPICHA; *Carduus* by P. H. DAVIS; *Centaurea* by G.

WAGENITZ; *Cirsium* by P. H. DAVIS & B. S. PARRIS; *Echinops* by I. C. HEDGE; *Onopordum* by A. DANIN.]

DITTRICH, M. Karpologische Untersuchungen zur Systematik von *Centaurea* und verwandten Gattungen. Bot. Jahrb. **88:** 70–162. 1968a.

———. Morphologische Untersuchungen an den Früchten der Subtribus Cardueae-Centaureinae (Compositae). Willdenowia **5:** 67–107. 1968b.

———. Morphologische und anatomische Untersuchungen an Früchten der Carduinae (Compositae). I. Morphologischer Teil. Candollea **25:** 45–67. 1970.

———. Cynareae—a systematic review. Chapter 36, pp. 999–1016 *in* V. H. HEYWOOD *et al.*, eds., Biology and chemistry of the Compositae. Academic Press, London, New York, and San Francisco. 1977.

———, F. PETRAK, K. H. RECHINGER, & G. WAGENITZ. Cynareae. *In:* K. H. RECHINGER, ed. Fl. Iran. 139a (October, 1979) & 139b (April, 1980). 2 vols. [*Arctium, Carduus, Cnicus, Cynara, Echinops, Onopordum, Silybum* by K. H. RECHINGER; *Cirsium* by F. PETRAK; *Centaurea* by M. DITTRICH & K. H. RECHINGER.]

DOMÍNGUEZ, X. A., A. GONZALEZ, M. A. ZAMUDIO, & A. GARZA. Taraxasterol from *Stevia Berlandieri* and *Cirsium texanum.* Phytochemistry **13:** 2001. 1974.

DON, G. The Linnean arrangement and its supplement. *In:* J. C. LOUDON, Loudon's Hortus Britannicus. London. 1830. [Source of early sections for the genus *Cirsium,* 330, 331, and possibly *Carduus,* 329, 330; *Onopordum,* 331. Other genera treated: *Centaurea,* 360–362; *Cynara,* 332; *Carthamus,* 332; *Silybum,* 330.]

———. A general history of the dichlamydeous plants. 4 vols. London. 1831–1838.

DUMORTIER, B. C. Florula belgica, operis majoris prodromus. Tornaci Nerviorum. 172 pp. 1827. [Source of the subtribes Carlineae, Centaureinae, Carduinae; see BRIZICKY for comment.]

DUNCAN, W. H., & J. T. KARTESZ. Vascular flora of Georgia. An annotated checklist. Athens, Georgia. 1981.

ELLIOTT, S. A sketch of the botany of South-Carolina and Georgia. 2 vols. Charleston, South Carolina. 1821–1824. [*Cirsium,* 7 spp., included in synonymy under *Cnicus,* pp. 268–272.]

FAHN, A. Secretory tissues in plants. x + 302 pp. London, New York, San Francisco. 1979. [*Carthamus, Centaurea, Silybum,* 64, 65.]

FERNALD, M. L. Gray's manual of botany. ed. 8. lxiv + 1632 pp. New York. 1950. [Key to Cynareae, 1537; *Arctium, Echinops, Carduus, Cirsium, Onopordum, Centaurea, Cnicus,* 1537–1545.]

FORCELLA, F., & H. WOOD. Sequential flowering of thistles (Cynareae, Asteraceae) in southern Australia. Austral. Jour. Bot. **34:** 455–462. 1986.

FRANKTON, C., & R. J. MOORE. Cytotaxonomy, phylogeny, and Canadian distribution of *Cirsium undulatum* and *Cirsium Flodmanii.* Canad. Jour. Bot. **39:** 21–33. 1961.

GAERTNER, J. De fructibus et seminibus plantarum. Stuttgart/Tübingen. 1788–1791. [Source of original description of *Silybum Marianum,* **2:** 378; source of accounts of various taxa in the Cardueae, including, among others, *Carduus, Centaurea, Cirsium, Cnicus, Echinops.*]

GIBBS, R. D. Chemotaxonomy of flowering plants. 4 vols. xxii + 2372 pp. Montreal & London. 1974. [*Cirsium, Centaurea, Carduus, Onopordum, Silybum, Arctium,* **1:** 94–96; *Centaurea, Cirsium, Silybum,* **2:** 1195, 1197.]

GLEASON, H. A., & A. CRONQUIST. Manual of vascular plants of northeastern United States and adjacent Canada. li + 810 pp. Boston. 1963. [*Arctium, Carduus, Cirsium, Silybum, Onopordum, Echinops, Centaurea, Cnicus,* 747–754.]

GOLDBLATT, P. Index to plant chromosome numbers 1975–1978. Monographs in systematic botany. Vol. 5. 553 pp. Missouri Botanical Garden. 1981. [Asteraceae, 70–141.]

———. Index to plant chromosome numbers 1979–1981. Monographs in systematic botany. Vol. 8. 427 pp. Missouri Botanical Garden. 1984. [Asteraceae, 52–109.]

———. Index to plant chromosome numbers 1982–1983. Monographs in systematic botany. Vol. 13. 224 pp. Missouri Botanical Garden. 1985. [Asteraceae, 31–59.]

GOLTZ, L. Honey and pollen plants. Part II. The thistles. Am. Bee Jour. **126:** 667–669. 1986. [*Cirsium, Silybum, Centaurea, Echinops, Onopordum, Carduus,* discussed as nectar sources.]

GRAY, A. Contributions to North American botany. I. Characters of new Compositae, with revisions of certain genera, and critical notes. Proc. Am. Acad. **19:** 1–73. 1884a.

———. Synoptical flora of North America. Vol. 1. Pt. 2. New York. 1884b. [Cynaroideae, including *Arctium, Carduus, Cirsium* (as *Cnicus*), *Onopordum, Silybum, Centaurea,* 396–407.]

GREAT PLAINS FLORA ASSOCIATION. Flora of Great Plains. vii + 1392 pp. Lawrence, Kansas. 1986. [Asteraceae, 838–1021, by T. M. BARKLEY; key to Cynareae, 844, 845; *Cirsium,* 908–914, by R. E. BROOKS; *Arctium,* 864, 865; *Carduus,* 895–897; *Carthamus,* 897, 898; *Centaurea,* 898–901; *Onopordum,* 979, 980, by R. L. MCGREGOR.]

GUPTA, R. D., & Y. S. MURTA. Studies on seed storage and viability in some weed seeds of family Asteraceae. Seed Res. New Delhi **14:** 115–125. 1986.*

GULYAS, S., & J. PESTI. Angaben zur Anatomie der Nektarien der *Centaureae.* Acta Biol. Szeged. **12:** 17–24. 1966.

HASLETT, B. G., T. GLEAVES, & D. BOULTER. N-terminal amino acid sequences of plastocyanins from various members of the Compositae. Phytochemistry **16:** 363–365. 1977.

HEGI, G. Compositae. Illustrierte Flora von Mittel-Europa **6**(2): 394–1367. *Taf. 269–273.* 1928–1929. [Genera of Cynareae, 807–992; includes *Echinops, Carlina, Arctium, Saussurea, Jurinea, Carduus, Cirsium, Silybum, Onopordum, Cynara, Serratula, Crupina, Rhaponticum, Centaurea, Carthamus, Cnicus.*]

———. Compositae. II. *Matricaria–Hieracium.* G. WAGENITZ *in* Illustrierte Flora von Mittel-Europa. 2. Auflage. Spermatophyta. Band 6. Angiospermae, Dicotyledones 4. vii + pp. 580–1483. 1987. [Includes Nachträge und Ergänzungen zum Nachdruck der 1. Auflage von Band VI/2 (1928/9), pp. 1352–1452. Genera of Cynareae, 1390–1413; includes genera noted above. Text of ed. 1 essentially unchanged; many black & white illustrations changed; new data largely in the Nachträge, 1353–1452.]

HEISER, C. B., & T. W. WHITTAKER. Chromosome number, polyploidy and growth habit in California weeds. Am. Jour. Bot. **35:** 179–186. 1948. [First reports for *Centaurea Calcitrapa,* $2n = 20$; *C. solstitialis,* $2n = 16$; *C. picris,* $2n = 26$; and *Silybum Marianum,* $2n = 34$. Counts for *Cirsium arvense* and *C. vulgare,* $2n = 34$, and $2n = 68$, respectively, confirmed earlier reports for these taxa.]

HERMOUT, V., & F. ŠORM. Chemotaxonomy of the sesquiterpenoids of the Compositae. *In:* J. HARBORNE & T. SWAIN, eds., Perspectives in phytochemistry. xi + 235 pp. London and New York. 1969. [Various members of Cardueae, 139–165.]

HESLOP-HARRISON, Y., & K. R. SHIVANNA. The receptive surface of the angiosperm stigma. Ann. Bot. II. **41:** 1233–1258. 1977. [*Centaurea,* 1240, listed as having a papillate stigmatic surface with unicellular papillae.]

HOFFMANN, O. Compositae. *In:* A. ENGLER & K. PRANTL, Nat. Pflanzenfam. IV. **5:** 87–391. 1894. [Tubifloreae–Cynareae, 312–333; *Cirsium, Carduus, Centaurea, Onopordum, Cnicus,* published Sept., 1893.]

HOWELL, J. T. Distributional data on weedy thistles in western North America. Leafl. West Bot. **9:** 17–29. 1959. [Early records noted for *Arctium, Carduus, Carthamus, Centaurea, Cirsium, Cnicus, Cynara, Echinops, Onopordum, Silybum.*]

ISLEY, D. Seed characteristics of weedy thistles. Assoc. Off. Seed Anal. Proc. **37:** 93–98. 1947. [*Cirsium, Cnicus, Onopordon* (sic.), *Silymbium* (sic.), *Carduus* keyed by seed characteristics.]

JANSEN, R. K., & J. D. PALMER. A chloroplast DNA inversion marks an ancient evolutionary split in the sunflower family (Asteraceae). Proc. Natl. Acad. Sci. U. S. A. **84:** 5818–5822. 1987.

JEFFREY, C. Notes on the Compositae: III. The Cynareae in East Tropical Africa. Kew Bull. **22:** 107–140. 1968.

———. Corolla forms in Compositae—some evolutionary and taxonomic speculations. Chap. 6. Pp. 111–118 *in* V. H. HEYWOOD *et al.*, eds., The biology and chemistry of the Compositae. London. 1977.

———. Compositae. Pp. 263–268 *in* V. H. HEYWOOD, consultant ed., Flowering plants of the world. New York. 1978.

JENSEN, S. R., B. J. NIELSEN, & R. DAHLGREN. Iridoid compounds, their occurrence and systematic importance in the angiosperms. Bot. Not. **128:** 148–180. 1975.

JOHNSON, M. F. Cynareae (Asteraceae) in Virginia: *Cirsium, Carduus, Onopordum.* Virginia Jour. Sci. **25:** 152–160. 1974.

———. Cynareae (Asteraceae) in Virginia: *Arctium, Centaurea, Cnicus.* Castanea **40:** 63–73. 1975.

——— & H. H. ILTIS. Preliminary reports on the flora of Wisconsin. No. 48. Compositae I—Composite family 1. Trans. Wisconsin Acad. Sci. **52:** 255–342. 1963.

KARTESZ, J. T., & R. KARTESZ. A synonymized checklist of the vascular flora of the United States, Canada and Greenland. Chapel Hill, North Carolina. 1980. [*Arctium,* 51; *Carduus, Carthamus, Carlina, Centaurea,* 62; *Cirsium* 65–67; *Echinops,* 71; *Onopordum,* 94; *Silybum,* 102.]

KITAMURA, S. Compositae Japonicae. Pars prima. Mem. Coll. Sci. Kyoto Univ. B. **13.** 1937. [Source of name of subfamily Carduoideae Kitamura, 5; tribe Cynareae, 5–212; *Echinops,* 14–18; *Carduus,* 32, 33; *Cirsium,* 33–134.]

LAMARCK, J. B. DE, & A. P. DE CANDOLLE. Flore Française. ed. 3. Paris. 1805. [Compositae. Vol. 4. pt. 1.]

LARSEN, K. Chromosome numbers of some European flowering plants. Bot. Tidsskr. **50:** 163–174. 1954. [*Centaurea Cineraria* L. reported as $2n = 18$; *Silybum Marianum* as $2n = 34$; confirmations of earlier counts.]

———. Chromosome studies in some Mediterranean and South European flowering plants. Bot. Not. **109:** 293–307. 1956.

LAVIALLE, P. Recherches sur le développement de l'ovaire en fruit chez les Composées. Ann. Sci. Nat. Bot. IX. **15:** 39–152. 1912.

LEONHARDT, R. Phylogenetisch-systematische Betrachtungen. I. Betrachtungen zur Systematik der Compositen. Österr. Bot. Zeitschr. **96:** 293–324. 1949. [Cynareae as most primitive tribe; Campanulaceae most closely related to the Asteraceae.]

LESSING, C. F. Synopsis generum Compositarum. xi + 473 pp. Berlin. 1832.

LÖVE, A., & D. LÖVE. Cytotaxonomical studies on boreal plants. Arkiv Bot. **31**(A): 1–22. 1944.

———. Chromosome numbers of Central and Northwest European plant species. Opera Bot. Lund. **5:** 1–581. 1961. [Compilation of chromosome numbers and sources for the Asteraceae, 339–362; *Carduus,* 339; *Cirsium,* 340; *Cynara, Silybum, Onopordum, Arctium,* 341; *Centaurea,* 342; *Carlina, Echinops, Cnicus,* 344.]

MABBERLEY, D. J. The plant-book. xii + 706 pp. Cambridge, England. 1987.

MACROBERTS, D. T. The vascular plants of Louisiana. An annotated checklist and bibliography of the vascular plants reported to grow without cultivation in Louisiana. Bull. Mus. Life Sci. Louisiana State Univ. Shreveport **6:** 1–165. 1984. [*Arctium minus,* 61; *Carduus nutans,* 62; *Cirsium altissimum, C. carolinianum, C. discolor, C. horridulum, C. Lecontei, C. muticum, C. Nuttallii, C. terrae-nigrae, C. undulatum, C. virginianum, C. vulgare,* 62; *Centaurea americana, C. Cyanus, C. maculosa,* 62; *Silybum Marianum,* 67.]

MCVAUGH, R. Flora Novo-Galiciana. Vol. 12. Compositae. 1157 pp. Ann Arbor, Michigan. 1984.

MEHRA, P. N., B. S. GILL, J. K. MEHTA, & S. S. SIDHU. Cytological investigations on the Indian Compositae. I. North-Indian taxa. Caryologia **18:** 35–68. 1965. [Chromosome numbers reported for certain taxa; Cynareae, 43; *Arctium Lappa, n* = 18; *Carduus nutans,* $2n$ = 40; *Cirsium arvense* (as *Cnicus arvensis* Hoffmann), *n* = 17; *Centaurea Cyanus, n* = 12; *Carthamus tinctorius, n* = 12.]

——— & P. REMANANDAN. Cytological investigations on Indian Compositae V. Tribes: Arctotidae, Cynareae, Calenduleae, and Mutisieae. Nucleus **19:** 8–12. 1976. [Two species of *Echinops* reported as *n* = 14; previous counts of *n* = 18 confirmed, meiosis was said to be normal and pollen fertility reported as 95 percent; *Carduus nutans* counted as *n* = 20, while "laggards and bridges" were said to disturb meiosis; *Cirsium arvensis* (as *Cnicus arvensis*) was reported as *n* = 17, in confirmation of earlier reports.]

MOORE, D. M., ed. Cardueae. *In:* T. G. TUTIN *et al.,* eds., Fl. Europaea **4:** 208–304. 1976. [*Arctium* by F. H. PERRING; *Carduus* (Key by M. L. ROCHA AFONSO), *Cnicus, Onopordum, & Silybum* by J. do AMARAL FRANCO; *Centaurea* by J. DÓSTAL; *Cirsium* by K. WERNER; *Echinops* by S. KOZUHAROV.]

MOORE, R. J., ed. Index to plant chromosome numbers 1967–1971. Reg. Veg. vol. 90. Utrecht. 1973.

——— & C. FRANKTON. Cytotaxonomic studies in the tribe Cynareae (Compositae). Canad. Jour. Bot. **40:** 281–293. 1962.

——— & ———. The thistles of Canada. Monograph No. 10. Research Branch, Canada Dep. Agr. 1974. [Includes treatments of *Echinops, Arctium, Cirsium, Carduus, Saussurea, Silybum, Onopordum, Centaurea, Cnicus* with discussions of economic uses.]

MORTON, J. K. Chromosome numbers in Compositae from Canada and the U. S. A. Bot. Jour. Linn. Soc. **82:** 357–368. 1981. [*Cirsium arvense,* $2n$ = 34; *C. discolor,* $2n$ = 20; and *Cnicus benedictus,* $2n$ = 22, reported.]

MULLER, J. Fossil pollen records of extant angiosperms. Bot. Rev. **47:** 1–142. 1981. [*Cirsium*-type pollen confirmed from the Pliocene, 100.]

NAKAI, T. Ordines familiae. Imperial University, Tokyo, Japan. 1943.

NOWAK, G., B. DROZDZ, W. KROSZCZYNSKI, & M. HOLUB. Sesquiterpene lactones XXX. Cynaropicrin in species of the subtribe Centaureinae. (In English; Polish summary.) Acta Soc. Bot. Poland. **55**(1): 17–22. 1986.

NUTTALL, T. The genera of North American plants. 2 vols. Philadelphia. 1818.

PARRA, O. Morfología de los granos de polen de los Compuestas Cynareas Chilenas. Bol. Soc. Biol. Concepción **42:** 89–96. 1970.*

PERSOON, C. H. Synopsis plantarum. Pars secunda. 657 pp. Paris. 1807.

PHILIPSON, W. R. The relationships of the Compositae, particularly as illustrated by the morphology of the inflorescence in the Rubiales and the Campanulatae. Phytomorphology **3:** 391–404. 1953.

———. Ovular morphology and major classifications of the dicotyledons. Bot. Jour. Linn. Soc. **68:** 89–108. 1974.

PODDUBNAJA-ARNOLDI, W. Ein Versuch der Anwendung der embryologischen Methode bei der Lösung einiger systematischer Fragen. I. Vergleichende embryologischen-zytologische Untersuchungen über die Gruppe Cynareae, Fam. Compositae. Beih. Bot. Zentralbl., Abt. 2, **48:** 141–237. 1931.

RADFORD, A. E., H. E. AHLES, & C. R. BELL. Manual of the vascular flora of the Carolinas. lxi + 1183 pp. Chapel Hill, North Carolina. 1968. [Compositae by H. E. AHLES. *Centaurea,* 1039–1041; *Carduus* (including *Cirsium*), 1041–1044; *Arctium,* 1045.]

RICKETT, H. W. Wildflowers of the United States. Vol. 2. The Southeastern States. Part 2. Pp. 606–612. 1966. [*Cirsium* pp. 606–610; *Carduus, Cnicus, Onopordum, Arctium* pp. 610–612. Color photos of *Cirsium altissimum, C. arvense, C. discolor, C. horridulum, C. Lecontei, C. muticum, C. Nuttallii, C. pumilum, C. repandum, C. virginianum*; *Carduus acanthoides, C. nutans*; *Arctium minus*; *Onopordum Acanthium.*]

ROBINSON, H. Some suggestions regarding the significance of chloroplast DNA variation in the Asteraceae. Phytologia **63**: 316–324. 1987.

RYDBERG, P. A. Flora of the Rocky Mountains and adjacent plains. Published by the author. New York. 1917. [Correct date is 1918, since the shipment of books was held up in a railroad strike and was not distributed until January, 1918, according to A. CRONQUIST (pers. comm.).]

———. Flora of the prairies and plains of central North America. New York. 1932.

SCOPOLI, J. A. Methodus Plantarum. 28 pp. Vienna. 1754.

———. Flora Carniolica. xxii + 607 pp. Vienna. 1760.

———. Flora Carniolica. ed. 2. 2 vols. (Vol. 1, lxxii + 448 pp.; vol. 2, 496 pp.) Vienna. 1772.

SEAMAN, F. C. Sesquiterpene lactones as taxonomic characters in the Asteraceae. Bot. Rev. **48**: 121–595. 1982.

SHISHKIN, B. K., & E. G. BOBROV, eds. Cynareae. (22 genera by 9 authors; in Russian.) Fl. URSS (SSSR). **27**: xxii + 760 pp. Moscow, Leningrad. 1962. [*Echinops*, 2–53, 58 species, by E. G. BOBROV; *Arctium*, 93–107, 8 species, by S. V. YUZEPCHUK. See BOBROV & CZEREPANOV, eds., vol. **28**, for other genera.]

SINGH, R. P., & A. K. PANDEY. Development and structure of seeds and fruits in Compositae-Cynareae. Phytomorphology **34**: 1–10. 1984.

SMALL, J. K. Manual of the southeastern flora. xxii + 1554 pp. New York. 1933.

SMALL, J. S. The origin and development of the Compositae. New Phytologist **18**(1&2): 1–35; (3&4): 65–89; (5&6): 129–176; (7): 201–234. London. 1919.

SMITH, E. B. An atlas and annotated list of the vascular plants of Arkansas, ed. 2. iv + 489 pp. Fayetteville, Arkansas. 1988. [Includes *Arctium minus*; *Carduus crispus*, *C. nutans*; *Centaurea* (3 spp.); *Cirsium* (7 spp.); *Cnicus benedictus*; *Silybum Marianum*.]

SOLBRIG, O. The tribes of Compositae in the southeastern United States. Jour. Arnold Arb. **44**: 436–461. 1963.

———. Subfamilial nomenclature of Compositae. Taxon **12**: 229–235. 1963.

SPACH, E. Histoire naturelle des végétaux. **10**: 10–15, 65–72. 1841. [Source of several subgeneric names in *Centaurea*.]

SPRAGUE, T. A. XXXV. Additions to the Index Kewensis. Bull. Misc. Inf. Kew **1925**: 312–314. 1925. [A list of species taken from Wallich's Catalogue and given descriptions by G. DON.]

STEPA, I. S. Ad cognitionem pollinis morphologiae generum nonnullerum tribus Cynareae familiae Compositae. Not. Syst. Geogr. Inst. Bot. Thbilissi. **20**: 54–62. 1959.

———. Morfologija pyl'cy roda *Cirsium* Mill. i blizkih rodov triby Cynareae (Compositae). Trudy Tbilis. Bot. Inst. **21**: 81–126. 1960.

STEUDEL, E. G. Nomenclator botanicus. ed. 1. Stuttgart, Tübingen. 1821–1824. [Later edition published in 1840.]

TAKHTAJAN, A. L. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. **46**: 225–359. 1980.

TUCCI, G. F., & F. MAGGINI. Ribosomal RNA genes in species of the Cynareae Tribe (Compositae) I. Protoplasma **132**: 76–84. 1986.

UNITED STATES DEPARTMENT OF AGRICULTURE. Common weeds of the United States. (Reprint.) Dover Publications, New York. 1971.

WAGENITZ, G. Compositae. Pp. 484–497 *in* H. MELCHIOR, ed., A. Engler's Syllabus der Pflanzenfamilien. ed. 12. II Band. Berlin. 1964.

———. Systematics and phylogeny of the Compositae (Asteraceae). Pl. Syst. Evol. **125**: 29–46. 1976.

WAGNER, H. Cynareae—a chemical review. Chapter 37 *in* V. H. HEYWOOD *et al.*, eds., Biology and chemistry of the Compositae. London. 1977.

WALLICH, N. Numerical list of dried plants in the East India Company's museum. London. 1831 [1828–1849]. [Often cited as "Wallich's Catalogue"; years of publication vary with number. Most of the "new species" listed in this catalogue are nomina nuda, since they lack descriptions. A number were later published by G. Don, 1831–1838. A list of these species can be found in Sprague, 1925.]

Wiegand, K. M., & A. F. Eames. The flora of the Cayuga Lake Basin. Cornell Univ. Agr. Exper. Sta. Mem. **92.** 491 pp. Ithaca, New York. 1926.

Willis, J. C. A dictionary of the flowering plants and ferns. ed. 7. Revised by H. K. Airy Shaw. Cambridge, England. 1966.

Wunderlin, R. P. Guide to the vascular plants of central Florida. Univ. Presses Florida. Tampa, and other cities, Florida. 1982.

Young, D. A., & D. S. Seigler, eds. Phytochemistry and angiosperm phylogeny. New York. 1981.

Young, D. J., & L. Watson. The classification of dicotyledons: a study of the upper levels of the hierarchy. Austral. Jour. Bot. **18:** 387–433. 1970.

Zohary, M. Evolutionary trends in the fruiting head of Compositae. Evolution **4:** 103–109. 1950.

Zwöfler, H. Preliminary list of phytophagous insects attacking wild Cynareae (Compositae) species in Europe. Commonwealth Inst. Biol. Control Tech. Bull. **6:** 81–154. 1965.

———. Mechanismen und Ergebnisse der Co-Evolution von phytophagen und entomophagen Insecten und höheren Pflazen. Sonderbände Naturwiss. Ver. Hamburg. **2:** 7–50. 1978.

Key to the Genera of Cardueae in the Southeastern United States

A. Achenes attached to the receptacle by the base; flowers all alike, marginal ones not enlarged.
  B. Heads 1-flowered, united into a spherical, secondary head. .... [*Echinops.*]
  B. Heads with more or less numerous flowers, not united into a secondary head.
    C. Receptacle fleshy, deeply alveolate, naked or only very shortly bristly; plants with strongly spiny-winged stem and tomentose herbage. . 4. *Onopordum.*
    C. Receptacle with scales or setae or densely bristly; plants without both stem strongly spiny winged and herbage tomentose throughout.
      D. Staminal filaments united below; leaves white mottled. ... 3. *Silybum.*
      D. Staminal filaments separate; leaves not white veined or variegated.
        E. Involucral bracts hooked at tip; leaves not bristly or spiny, the lower broadly ovate and mostly cordate; style branches partly distinct. ... . 5. *Arctium.*
        E. Involucral bracts not hooked; leaves bristly or spiny on the margin, lanceolate or narrow; style branches coherent, commonly with a pubescent ring at base.
          F. Pappus bristles plumose; stem not conspicuously spiny winged (except in *C. vulgare*). .... 1. *Cirsium.*
          F. Pappus bristles barbellate, not plumose; stem conspicuously spiny winged. .... 2. *Carduus.*
A. Achenes obliquely or laterally attached to the receptacle; marginal flowers often enlarged and neutral, appearing ray-like, occasionally undifferentiated from inner florets.
  G. Achenes with 10 horny teeth at the summit, and with a biseriate pappus of 10 long awns alternating with 10 shorter inner ones; leaves prickly margined; flowers yellow. .... 7. *Cnicus.*
  G. Achenes without horny apical teeth, and with a pappus of several series of short (seldom elongate) scales or bristles, or the pappus wanting; leaves not prickly; flowers in most species anthocyanic (or white), seldom yellow... 6. *Centaurea.*

Subtribe CARDUINAE Dumortier, Fl. Belg. Prodr. 72. 1827.

1. **Cirsium** Miller, Gard. Dict. Abridg. ed. 4. **1:** ord. alph. 1754, emend. Scopoli, Fl. Carniol. ed. 2. 123. 1772.

Biennial or perennial [annual] herbs. Stems to 2.5 m tall, branched or simple, arachnoid-tomentose to glabrous, unarmed or spiny winged, wings triangular with a short apical spine. Leaves sessile to long petiolate; blades lanceolate to oblanceolate, the upper surface glabrescent or setaceous [densely pubescent], glandular, or glandular-pubescent, lower surface glabrescent or pubescent along the primary veins to white-tomentose throughout, glands capitate or punctate, hairs crispate or sinuate, multicellular; margins entire to more often incised or laciniate, weakly to strongly spiny. Capitula (heads) homogamous or heterogamous, discoid, ovoid to globose, terminal or axillary, solitary or in clusters of 3 to several heads on short to somewhat elongate peduncles [sessile]. Involucre ovoid, to ca. 7 cm high and ca. 9 cm wide, bracts imbricate, multiseriate, linear-lanceolate to lanceolate, acute to acuminate, often spine tipped, usually with a simple apical spine, adpressed to reflexed, glabrous to sparsely pubescent [arachnoid-pubescent], often with a glutinous dorsal ridge (vitta), entire or ciliate [lacerate]. Receptacle flat to subconic, scales numerous, setaceous. Flowers perfect (rarely imperfect and then the heads functionally so and the plants partly or wholly dioecious). Corollas tubular, actinomorphic, white, cream-yellow, lavender, purple, or garnet red [red], glabrous or sparsely glandular, tube narrow, elongate, throat short, undivided, lobes linear to lanceolate, elongate. Staminal filaments glabrous to more often papillose-hairy, anthers white or stramineous, saggitate, apical appendage acute, small. Styles smooth below a distinct collar of hairs, branches papillate, scarcely divergent, narrowly truncate to acute. Achenes 3–6 mm, basifixed or nearly so, glabrous, smooth, oblong, compressed, gibbous, with a distinct, apical margin surrounding a subconical central projection. Pappus of several rows of distinctly plumose setae, basally fused, deciduous as a ring [or persistent]; the inner setae somewhat longer than the outer and simple, lanceolate, occasionally flattened and ciliate towards apex; pappus of outermost florets often with fewer, minutely barbellate or scabrous setae. LECTOTYPE SPECIES: *Cirsium heterophyllum* (L.) Hill. (*Carduus heterophyllus* L.) = *Cirsium helenioides* (L.) Hill; see Britton & Brown, Illus. Fl. No. United States, Canada. ed. 2. **3:** 548. 1913; Britton & Millspaugh, Bahama Flora, 458. 1920; R. McVaugh, Flora Novo-Galiciana, 229. 1982. Werner treated *Cirsium heterophyllum* as a synonym of *C. helenioides* (L.) Hill in *Flora Europea.* (Name Latin, from *cirsion,* thistle, used by Dioscorides, from *kirsos* or *cirsos,* a swollen vein, which it was said to cure; see Loudon; Fernald; Correll & Correll; Munz.)—THISTLE, PLUMED THISTLE.

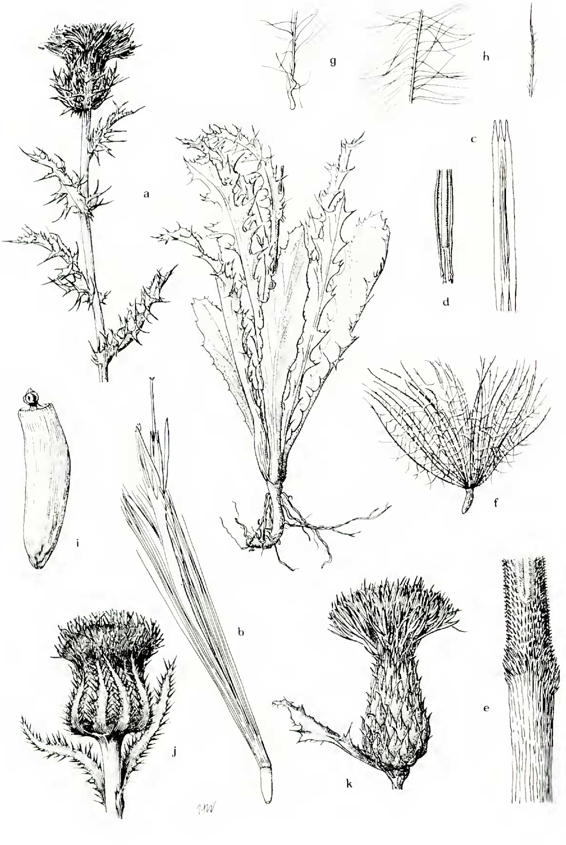
Tenuous morphological distinctions and a misunderstood nomenclatural history have led authors to treat members of *Cirsium* as representatives of both *Carduus* (Elliott; Nuttall; Radford *et al.*) and *Cnicus* (Gray, 1874; Pammel, 1901). Linnaeus did not recognize *Cirsium,* but described the species later treated as *Cirsium* as representatives of *Carduus.* The year following the publication of *Species Plantarum,* Miller proposed *Cirsium* on the basis of characteristics of the spines on the leaves and the lack of spines on the "cup of the flower" (i.e., involucre). Miller used polynomials under his generic descriptions until the 1768 edition of *The Gardener's Dictionary* (see Druce for commentary), yet in this edition Miller merged *Cirsium* with *Carduus.* Because of this, it was Scopoli (1772) who provided the first binomials in *Cirsium* and who noted the plumose pappus as a distinguishing character for the genus. Adanson was wrongly credited as the author of *Cirsium* for his realignment of *Cnicus* Tournefort (*Cnicus* L. is now a conserved name). Primarily on the basis of characters of the achene, Cassini, Lessing, and De Candolle considered *Cirsium* to be closely related to *Carduus,* but distant from *Cnicus.* Bentham and Asa Gray (1874) both included *Cirsium* in *Cnicus,* but Hoffmann maintained its generic status. Dittrich (1977) assigned *Cirsium* and *Carduus* to the tribe Cardueae (subtribe Carduinae Dumort.) and aligned them with *Modestia* Charadze & Tamamshian (a genus of three species of Central Asia) and *Silybum* on the basis of achene characters (apical plate, pappus, and detachment area).

While the division between *Cirsium* and *Carduus* has long been noted as somewhat arbitrary (cf. Scopoli, 1772; McVaugh) and various authors (e.g., Correll & Johnston; Willis) have suggested that *Cirsium* should be included within *Carduus.* Ahles in Radford *et al.* (1968) is the only recent author who has adopted this position. Recent floras of Europe (e.g., *Flora Europaea, Flora of Turkey, Flora Iranica*) and the Orient have maintained *Cirsium* and *Carduus* as separate genera.

A number of sectional names have been proposed for *Cirsium* since Dumortier first subdivided the genus into sections *Eriolepis* (Cass.) Dumort. (involucres woolly), *Onotrophe* (Cass.) Dumort. (involucres spiny), and *Cirsiotypus* Dumort. (involucres unarmed). Dumortier was followed shortly by Duby, who borrowed on De Candolle's unpublished material and described the sect. *Epitrachys* DC. ex Duby (leaves with upper surface spiny; flowers purple).

In a treatment that has gone largely unrecognized, George Don (in Loudon) divided *Cirsium* into seven sections: *Solitaria* (leaves decurrent; flowers red, heads subsolitary), *Polyanthema* (leaves decurrent; flowers red, heads aggregated), *Leucanthum* (leaves decurrent; flowers whitish), *Eriophora* (leaves sessile; flowers red, heads subsolitary), *Aggregata* (leaves sessile; flowers red, aggregated), *Chrysantha* (leaves sessile; flowers yellow or white), and *Dubia.* Don's sect. *Eriophora* contained several species found in the southeastern United States (*C. discolor, C. altissimum, C. muticum* Michaux, *C. virginianum* (L.) Michaux, *C. arvense* (L.) Scop.), as well as the species later chosen as lectotype of the genus. Don's treatment of other families had closely followed De Candolle's accounts published in his *Prodromus,* but his treatment of the Compositae preceded De Candolle's by several years.

De Candolle recognized six sections: *Lophiolepis* (Cass.) DC., *Eriolepis, Orthocentron* (Cass.) DC., *Corynotrichum* DC., *Cephalonoplos* DC., and *Onotrophe* DC. The last section contained several species (*C. repandum* Michaux, *C. horridulum* Michaux, *C. muticum, C. virginianum*) from the southeastern United States, and, along with Don's sect. *Eriophora,* is currently placed in synonymy under sect. Cirsium. Koch, who claimed to have based his treatment on a manuscript of De Candolle's treatment of Compositae for the *Prodromus,*


g
h
a
c
d
f
i
b
e
j
k
VW

attributed two sections to De Candolle (*Epitrachys, Chamaeleon*) that De Candolle did not recognize, and erected yet two others (*Breea* (Less.) Koch and *Picnomon* (Cass.) Koch), each of which contained a single species (*C. arvense* and *C. acarna* DC., respectively). Koch's sect. *Chamaeleon* was later placed in synonymy under sect. CIRSIUM, and his sect. *Breea* is considered to be a synonym of sect. CEPHALONOPLOS, a section set aside for dioecious species.

Although Bentham (1873a) did not produce a sectional treatment of *Cirsium,* Hoffmann, whose treatment of the Compositae bore many similarities to Bentham's, recognized seven sections of *Cirsium*: *Notobasis* (Cass.) Hoffm., *Cephalonoplos* DC., *Epitrachys* DC. ex Duby, *Chamaeleon* DC. ex Koch, *Erythrolaena* Don in Sweet, *Ptilostemon* (Cass.) Hoffm., *Lamyra* (Cass.) Hoffm., and *Ancathia* (DC.) Hoffm.

Petrak (1917), the most recent monographer of *Cirsium,* considered the American species to be members of subgenus *Eucirsium* (= CIRSIUM) in which he recognized six sections for the North American taxa: *Cirsiopsis* Petrak, *Mastigophyllum* Petrak, *Dermatolepis* Petrak, *Echenais* (Cass.) Petrak, *Onotrophe* and *Erythrolaena* (see Ownbey & Hsi). The nearly 15 indigenous species known from the Southeast (excluding two European introductions) were placed in three subsections of sect. *Onotrophe* (Petrak, 1917; Frankton & Moore, 1969; Ownbey & Olson), a section later considered to be a synonym of sect. CIRSIUM (Petrak, 1979).

The two naturalized European species (*Cirisum arvense* (L.) Scop. and *C. vulgare* (Savi) Tenore) are not considered to be closely related to the native species of the Southeast. Werner included *C. vulgare* in sect. *Eriolepis,* but Petrak (1979) placed this species in sect. *Epitrachys* subsect. *Lanceolata* Petrak. While the name *Epitrachys* may more closely characterize the group of taxa included under this name, Petrak's description of *Epitrachys* and Werner's description of sect. *Eriolepis* are not easily distinguished. As treated by Werner, the sect. CIRSIUM includes *C. helenioides* (L.) Hill under which he synonymized *C. heterophyllum,* the taxon previously designated as the lectotype species for the genus (see above). *Cirsium arvense* was retained in sect. CEPHALONOPLOS DC. by both Petrak (1979) and Werner.

Of the nearly 75 species of *Cirsium* recognized in the continental United States, only 12 to 15 are native to the Southeast. Many are biennials or mono-

FIGURE 1. **Cirsium.** a–i, *C. vittatum*: a, small flowering plant, base of plant to right, upper part with flowering head to left, × ½; b, flower, showing protruding stamens and style, × 2; c, three of the five anthers from within, the central one in more detail, × 4; d, base of an anther from within to show appendages, filament removed, × 10; e, detail of style, showing stylar brush at middle and lowermost part of united style arms with stigmatic line, × 30; f, achene with pappus, × 1; g, h, basal, central, and distal portions of a single pappus filament, × 4; i, achene from which pappus has become detached, × 5. j, *C. horridulum*: flowering head, showing conspicuous false involucre, × ½. k, *C. Lecontei*: flowering head, the cobwebby hairs omitted, × 1.

carpic taxa that need three to five years to come to flowering and fruition. Petrak (1917) treated the southeastern taxa in three subsections (*Odorata, Campanulata,* and *Acanthophylla*) of sect. ONOTROPHE DC. Taxa of subsections *Odorata* and *Campanulata* tend to inhabit the Atlantic and Gulf Coastal Plains and are often associated with salt or fresh marshes, bogs, savannas and pine barrens. The subsection *Acanthophylla* includes taxa often found in woodlands, thickets, and pasture areas of the Piedmont of Georgia and the mountains of Kentucky, Tennessee, and Arkansas. Cytological studies (Ownbey & Hsi; Ownbey & Olson; Moore & Frankton, 1969) have indicated that species of subsect. *Odorata* have chromosome numbers of $2n = 30$ and above, while those of subsections *Campanulata* and *Acanthophylla* have lower chromosome numbers ($2n = 18, 20$).

Recent treatments of the species of *Cirsium* in the eastern and southeastern United States have followed Petrak's taxonomic system, except for a realignment of two species at the subsectional level (Ownbey & Olson). The transfer of *C. Lecontei* Torrey & Gray and *C. repandum* Michaux from subsect. *Campanulata* to subsect. *Odorata* was made on the basis of their apparent cytological homogeneity with the other species (*C. horridulum* Michaux, *C. pumilum* (Nutt.) Sprengel, *C. vittatum* Small) of the latter subsection. The transfer of *C. repandum* and *C. Lecontei* left *C. Nuttallii* DC. the lone member of subsect. *Campanulata,* a group initially characterized by oblong-cylindrical or campanulate capitula.

Cirsium repandum, C. Nuttallii, and *C. Lecontei* are morphologically similar species often found growing in sandy soils of pine barrens and savannas of the Coastal Plain. *Cirsium Lecontei* appears to inhabit somewhat wetter habitats (edges of swamps, peat bogs, low, moist meadows) than the other two species, which occur in open pine woodlands, on sand ridges, and along roadsides. All three species flower primarily from mid-June to mid-September (Cronquist, 1980; Radford *et al.*, 1968). No occurrence of hybridization among these species has been reported. Moore & Frankton (1969) considered *Cirsium repandum* and *C. Lecontei* to be uniform species that show characteristics of other species groups, but remain strikingly distinct. They suggested that *C. repandum* may have developed from hybridization between the similar more northern species *C. pumilum* and the *C. horridulum* complex (Moore & Frankton, 1969), a group that Petrak (1917) and Moore & Frankton believed to be unrelated in origin to other North American species.

Several taxa (e.g., *C. horridulum, C. Smallii* Britton, *C. vittatum*), recognized as series *Horridula* of subsect. *Odorata,* form a distinct group easily recognized in the field by the presence of a large false involucre (Moore & Frankton, 1969). Elements of this complex, distinguished from one another by one or two subtle characters (Cronquist, 1980), can be found along the Atlantic and Gulf Coastal Plains from Maine to Mexico in the sandy soil of low pine woods, savannas, or along the edges of fresh or salt marshes.

Chromosome numbers of $2n = 30$ were reported for *C. pumilum* and *C. repandum,* $2n = 32$ for both *C. Lecontei* and *C. horridulum,* and $2n = 32, 34$ $(33, 35)$ for *C. vittatum* (Ownbey & Olson). Moore & Frankton (1969) reported $2n = 28$ for *C. Lecontei* and suggested that this species arose from a past hybridization between stock of the series *Horridula* and *C. Nuttallii* (subsect. *Campanulata*). Two chromosome numbers ($2n = 24$ and $2n = 28$) were reported for *C. Nuttallii,* and probable accessory chromosomes were observed in association with 12 bivalents in a plant from Florida, yet normal meiosis was noted among 14 bivalents in plants from Louisiana. Ownbey & Olson investigated plants of *C. Nuttallii* from populations in Florida, Georgia, and South Carolina and found the chromosome number to be consistently $2n = 24$, except for one plant from Georgia with a chromosome number of $2n = 26$.

Included in a third subsect., *Acanthophylla,* were four species from the Southeast (*C. altissimum* (L.) Sprengel, *C. discolor* (Muhl.) Sprengel, *C. muticum* Michaux, *C. virginianum* (L.) Michaux). This subsection was differentiated primarily by ovate to ovate-globose capitula and weakly spiny involucres (Petrak, 1917). Later, *C. carolinianum* (Walter) Fern. & Schub. and *C. terrae-nigrae* Shinners (= *C. Engelmannii* Rydb.; see Shinners, 1964) were added to this subsection (Ownbey & Olson). Many of the taxa comprising the subsection inhabit inland woods, thickets, and pasture areas of higher elevations and, in some cases, have become ready colonizers of disturbed areas. *Cirsium muticum* is found in swamps and moist woods from central Canada to New Brunswick, south to the Gulf Coast, and west to eastern Texas. *Cirsium discolor* occurs in drier habitats, mostly thickets and grasslands, from New England south along the Atlantic Coast to North Carolina, west to Tennessee, and north to Minnesota. The closely related *C. altissimum* (L.) Spreng. occupies slightly more shaded, but otherwise similar habitats to those of *C. discolor* (see, Ownbey, 1964). The distributional range of *C. altissimum,* from southern New York to northern Florida, west to the Dakotas and Texas, is more southerly than that of *C. discolor.* According to Frankton & Moore (1963), this southern extension of *C. altissimum* may be attributed to the reduction of the diploid chromosome number from 20 to 18 and the coincident plasticity that produced the southern phenotypes of *C. altissimum,* which are sometimes recognized as species.

Subsection *Acanthophylla* appears to be morphologically and cytologically homogeneous. At least three species (*Cirsium carolinianum. C. muticum, C. discolor*) have chromosome numbers of $2n = 20$. Extra chromosomes arising from meiotic irregularities and triploid populations have been reported for *C. muticum* (Frankton & Moore, 1963; Ownbey & Olson), which is known to hybridize with *C. discolor* (Ownbey, 1951; Bloom). In turn, *C. discolor* has been shown to hybridize with *C. altissimum,* $2n = 18$ (Ownbey, 1964), the two not easily distinguished in parts of their ranges (Davidson) and considered to be conspecific by some authors (e.g., Gray, 1884b; Wiegand & Eames). More than 98 percent of both pollen and achenes produced by the progeny of the cross between *C. discolor* and *C. altissimum* aborted before maturation, yet rare instances of introgression were reported (Ownbey, 1964). A similar pattern was found in the hybrid progeny of the *C. muticum* × *C. discolor* crosses. In this case, the hybrids produced less than three percent fully formed pollen (vs. over 90 percent for the parental species), and less than five percent of the flowers in hybrids produced mature achenes; yet some evidence of introgression of *C. discolor* into *C. muticum* was reported (Ownbey, 1951).

On the basis of concepts set forth in an earlier paper (Moore & Frankton, 1962b), Frankton & Moore (1963) considered *Cirsium discolor* and *C. altissimum* to be slightly more advanced morphologically than *C. muticum,* because of the number of pappus setae and the length of the corolla tube relative to the rest of the corolla. Petrak placed *C. discolor* and *C. altissimum* in the series *Altissima* and *C. muticum* alone in the series *Mutica,* an arrangement with which Frankton & Moore (1963) concurred. More recently, these three species, along with *C. Engelmannii* Rydb. (*C. terrae-nigrae* Shinners) and *C. carolinianum,* were grouped in the series *Altissima* (Ownbey & Olson).

Cirsium virginianum (L.) Michaux, a species of the Atlantic Coastal Plain that inhabits savannas, bogs, and wetlands from New Jersey to northern Florida, is morphologically similar to *C. carolinianum,* a species that occurs in open woods on dry, sandy soils from southern Ohio to the mountains of North Carolina, northwestern Georgia, Alabama, Arkansas, Louisiana, and eastern Texas. *Cirsium virginianum* has been reported to have chromosome numbers of $2n = 28$ (Ownbey & Olson; Moore & Frankton, 1969) and $n = 11$ (Jones, 1968), while *C. carolinianum* has been reported as $2n = 20$ (Ownbey & Olson) and $n = 11$ (Jones, 1970). Ownbey & Olson included *C. carolinianum* in series *Altissima,* but left *C. virginianum* in series *Virginiana* where it was initially placed by Petrak. *Cirsium virginianum* was not considered by them to be closely allied to other species of the Southeast, and its relationships to other North American species were considered to be obscure (Ownbey & Olson).

Cirsium arvense (L.) Scop. is a widespread, pernicious weed that occurs in fields and wasteplaces across the northern half of Europe and the United States. It extends south into Iowa (Pammel; Hayden) and Kansas (Barkley) and west to California, but it only skirts the northern part of the Southeast: northwestern North Carolina, northern Tennessee, and northwesternmost Arkansas (E. B. Smith). This species causes considerable losses in agricultural yields (Hayden; Hodgson, 1958, 1968; U. S. Dep. Agr.), and its control has been the subject of studies too numerous to be accounted for in this treatment (for partial reviews, see Haggar *et al.*; Hodgson, 1968).

The separation of "sexes" in *Cirsium arvense* was first noted by T. Smith (1822), who described in detail the morphological differences between what he considered to be separate "male" and "female" plants. Correns (1916) more accurately described the imperfectly dioecious nature of this species and noted staminate plants bearing seeds of sexual origin. Correns's findings were confirmed by Delannay (1977), who showed that the stigmas of staminate plants are narrower and more elongated and the stigmatic papillae less well developed than on carpellate plants. According to Delannay, the result of these differences is less retention and germination of pollen on the staminate plants. Both Delannay (1977, 1979) and Lloyd & Myall upheld Correns's proposal that dioecy in *Cirsium* evolved from gynodioecy, a condition common to many European species of *Cirsium* (e.g., *C. palustre*; Delannay, 1979). While early studies (Bakker; Correns; Groh; Lloyd & Myall) reported very few occurrences of "hermaphrodites" or strict dioecy among populations of *C. arvense,* Kay took into account that populations of this species differentiate into clones with pollen-bearing flowers and clones with strictly carpellate ones and found that

15 percent of the pollen-bearing clones among three populations in southern Britain were perfect-flowered plants that produced from ten to 65 seeds per capitulum. Another 11 percent were "subhermaphrodites" that produced two to ten seeds per capitulum. Both "hermaphrodites" and "subhermaphrodites" had high seed viability, but experiments in self-pollination resulted in low seed set among the perfect-flowered plants.

Williams studied the germination of achenes of five *Cirsium* species and reported that of those studied *C. arvense* was the most variable, with the percent of germination ranging from 13.4 to 24 in four separate studies. Williams also noted that the achenes of many thistles are commonly parasitized by beetle larvae, fruit flies (*Urophora* sp.), and rusts (*Puccinia* sp.). Guyot & Guillemat recorded a considerable decrease in viability of *C. arvense* seeds over a period of five years (less than ten percent germination after five years). Kumar & Irvine reported an increase in germination rate in *Cirsium arvense* achenes in response to prechilling, photoperiod (eight hours of light), and higher temperatures (30°C). Similar results were reported by Amor & Harris in populations found in Victoria, Australia. Allelopathic properties have been attributed to *C. arvense* by several authors (Amor & Harris; Bendall; Helgeson & Konzak; Stachion & Zimdahl).

Cirsium vulgare, a wind-dispersed, monocarpic, tetraploid ($2n = 68$) weed introduced from Eurasia, is widely established in disturbed areas in much of North America. Although primarily an insect-pollinated outcrossing plant, self-pollination or apomixis has been shown to produce viable, if somewhat fewer, seeds. Achenes produced by either self-pollinated flowers or apomixis were significantly heavier than achenes produced by cross-pollinated flowers. In addition, achenes produced by cross-pollination germinate more slowly, and fewer seedlings survive their first year, than achenes produced by apomixis or self-pollination (Van Leeuwen, 1981b). This led Van Leeuwen to propose that achenes produced by cross-pollination are better dispersed and perhaps better equipped genetically (i.e., genetically more differentiated) to colonize areas apart from the parental plants than are achenes produced otherwise. Predispersal seed predation by birds, mice, and insects (particularly *Cheilosia grossa* and *Epiblema scutulana*) resulted in an average loss of seven percent of the achenes in populations of *C. vulgare*. Stem predation by rabbits and stem-boring insects brought about an average 38 percent loss of flowering heads on these plants (Van Leeuwen, 1981a, 1983). De Jong & Klinkhammer proposed a different hypothesis for the effects of microorganisms on the germination of seeds of *C. vulgare*.

The range of chromosome numbers from $2n = 34$ to $2n = 18$ among species of *Cirsium* has been proposed to be an aneuploid reduction series brought about by translocations between non-homologous chromosomes (Frankton & Moore, 1961; Moore & Frankton, 1962a; Ownbey & Hsi; Bloom). Intraspecific variation in chromosome numbers and accessory chromosomes are considered to be common (Frankton & Moore, 1963; Moore & Frankton, 1962a; Ownbey *et al.*; Pinkava & Keil). American species have been consistently reported to be diploids, while species introduced from Europe (*C. arvense, C. vulgare*) are known to be polyploids (Bloom). Triploid, tetraploid, and hexaploid species (all with multiples of 17 chromosomes) have been noted among Japanese species (Aishima, Arano). Taxa from the putative center of origin in Eurasia have been reported as diploids ($2n = 34$) or polyploids (Moore & Frankton, 1962a; Ownbey, Raven, & Kyhos; Bloom). Moore & Frankton (1962a) suggested that the European species of *Cirsium* are on the base level of cytological evolution, since they share a base chromosome number of 17.

Few investigations have been made of the phenolic compounds of *Cirsium* species. The flavonoids tricin-5-O-glucoside, quercetin-3-O-digalactoside and quercetin-3-O-rhamnoglucoside were reported as major constituents in *C. arvense* (Wallace). Shelyuto and colleagues (1970, 1972b) isolated apigenin, luteolin, apigenin-7-O-glucoside, apigenin-7-O-rhamnoglucoside and 3-O-methylkaempferol from *C. arvense* (see Wagner for review). The flavonoid cirsimaritin, first found in *C. brevistylum,* was determined to be a minor constituent of *C. arvense,* but was not found in *C. edule, C. undulatum,* or *C. vulgare* (Wallace & Bohm). The flavonoids kaempferol-3-O-glucoside, quercetin-3-O-glucoside, quercetin-3-O-galactoside, apigenin-7-O-diglucoside, and genkwanin-4'-O-glucoside were reported for *C. lanceolatum* (L.) Hill (McGowan & Wallace[3]). The phenolic acids p-coumaric, caffeic, ferulic, p-hydroxybenzoic, protocatechuic and vanillic were also reported for *C. lanceolatum* (McGowan & Wallace). Taraxasterol was found in *C. texanum,* but tests for alkaloids and sesquiterpene lactones were negative for this species (Domínguez *et al.*). Taraxasterol and triterpenes are known from *C. arvense* (Dutta *et al.*), and stigmasterol has been reported from *C. oleraceum* (L.) Scop. (Piatak & Eichmeier). Alkaloids of unknown structure have been found in *C. arvense* and in 12 other species of *Cirsium* (Willaman & Schubert; Willaman & Li).

REFERENCES:

Under tribal references see BARKLEY; BENTHAM, 1873a; BOBROV & CZEREPANOV; BRIZICKY; DE CANDOLLE; CASSINI; CORRELL & JOHNSTON; CRONQUIST, 1980; DITTRICH, 1977; DOMINGUEZ *et al.*; DON; DUMORTIER; ELLIOTT; GOLDBLATT, 1981, 1984, 1985; GRAY, 1884a, 1884b; HEGI, 1928–1929, 1987; HOFFMANN; ISLEY; LESSING; MACROBERTS; MCVAUGH; MORTON; MULLER; NUTTALL; PERSOON; RADFORD *et al.*, 1968; RICKETT; SMALL, 1933; E. B. SMITH; STEPA, 1959, 1960; UNITED STATES DEP. AGR.; WAGNER; and WILLIS.

AHLES, H. E., C. R. BELL, & A. E. RADFORD. Species new to the flora of North or South Carolina. Rhodora **60:** 10–32. 1958. [*Cirsium arvense.*]

AIRY SHAW, H. K. On *Cirsium lanceolatum* Hill and *C. lanceolatum* (L.) Scop. Not. Syst. Paris **13:** 55–58. 1947.

AISHIMA, T. Chromosome numbers in the genus *Cirsium.* I. Bot. Mag. Tokyo **48:** 150–

---

[3] McGowan & Wallace cited [Ahles *in*] Radford *et al.* as their source for this specific name; both *Cirsium lanceolatum* and *Cirsium vulgare* (Savi) Tenore were listed at the end of Ahles's treatment of *Carduus lanceolatus* L. *Cirsium vulgare* is probably the correct name of the species McGowan & Wallace studied, since *Cirsium lanceolatum* is a European species unknown in America, and the plant material used by McGowan & Wallace was collected in Jackson County, North Carolina. The name *Cirsium lanceolatum* (L.) Hill was misapplied by Small (1933) to *Cirsium vulgare* (Savi) Tenore and, apparently for this reason, was cited by Ahles (in Radford *et al.*) in his account of this species. (For commentary on this nomenclatural problem see Airy Shaw; Arenas, 1947.)

151. 1934. [Chromosome numbers for thirty species in 8 series were 17 or multiples thereof. Author suggests 17 as base number for the genus.]

Amor, R. L., & R. V. Harris. Distribution and seed production of *Cirsium arvense* (L.) Scop. in Victoria, Australia. Weed Res. **14:** 317–323. 1974.

Arenas, J. À propos de *Cirsium lanceolatum* Hill et de *Cirsium lanceolatum* Scop. Not. Syst. Paris **13:** 59–60. 1947.

———. Les Composées-Cynarocephales de Belgique. Bull. Jard. Bot. Bruxelles **24**(4): 255–274. 1954.

Areno, H. The karyotype analysis and its karyo-taxonomic considerations in some genera of subtribe Carduinae. Jap. Jour. Genet. **32:** 323–332. 1957. [All members of *Cirsium* classified into 3 types from the viewpoint of the karyotype, and *Cirsium* type is subdivided into 3 subtypes that agree with Kitamura's taxonomic systems.]

Bakker, D. A comparative life-history study of *Cirsium arvense* (L.) Scop. and *Tussilago Farfara* L., the most troublesome weeds in the newly reclaimed polders of the former Zuiderzee. Brit. Ecol. Soc. Symp. **1:** 205–222. 1960.

Beaman, J. H., & B. L. Turner. Chromosome numbers in Mexican and Guatemalan Compositae. Rhodora **64:** 271–276. 1962. [*Cirsium Skutchii* from Guatemala reported as $n = 17$.]

Bendall, G. M. The allelopathic activity of California thistle (*Cirsium arvense*) in Tasmania. Weed Res. **15:** 77–81. 1975.

Bloom, W. L. Chromosomal differentiation between *Cirsium discolor* and *C. muticum* and the origin of supernumerary chromosomes. Syst. Bot. **2:** 1–13. 1977. [Analyses of F_1 hybrids between these taxa indicate that the chromosome arrangements of these species differ by two or three translocations and one paracentric inversion.]

Bohlmann, F., & W. R. Abraham. Aplotacene epoxide from *Cirsium hypoleucum.* Phytochemistry **20**(4): 855, 856. 1981.

Britton, N. L., & C. F. Millspaugh. The Bahama flora. Published by the authors. New York. 1920. [*Cirsium Smallii* Britton described; *C. pinetorum* Small placed in synonymy.]

Charadze, A. L. *Cirsium.* (In Russian.) *In:* B. K. Shishkin & E. B. Bobrov, eds., Flora URSS. **27:** 51–215. 1963.

Clute, W. N. The meaning of plant names. XLII. The thistles. Am. Bot. **35:** 72–76. 1930.

Correll, D. S., & H. B. Correll. Flora of the Bahama Archipelago. (50) + 1692 pp. *frontisp.* Vaduz. 1982. [*Cirsium vittatum* (illustrated) and *C. horridulum,* 1466–1468; fresh stems of latter species chopped up for salads or "soaked in acetic acid in the manner of pickles."]

Correns, C. Untersuchungen über Geschlechtsbestimmung bei Distelarten. Sitz-ber. Acad. Wiss. Berlin **20:** 448–477. 1916.

Czapik, R. Karyological studies in species of *Cirsium* Mill. em. Scop. occurring in Poland. (In Polish.) Acta Soc. Bot. Polon. **27:** 483–489. 1958.

Dabydeen, S. Natural hybridization in the genus *Cirsium*: *C. Flodmanii* × *C. undulatum.* Rhodora **89:** 369–373. 1987.

Dandeno, J. B. The parachute effect of thistle down. Science II. **22:** 568–572. 1905.

Davidson, R. A. Initial biometric survey of morphological variation in the *Cirsium altissimum–C. discolor* complex. Brittonia **115**: 222–241. 1963.

Davis, D. E. The thistle [*Cirsium horridulum.*] No. 1 pasture weed? Highlights Agr. Res. Ala. Sta. **8**(1): 13. 1961.*

Davis, P. H., & B. S. Parris. *Cirsium. In:* P. H. Davis, ed., Fl. Turkey **5:** 370–412. 1975.

Delannay, X. Cytological study of dioecy in *Cirsium arvense.* Phytomorphology **27:** 419–425. 1977.

———. La gynodioecie dans le genre *Cirsium* Miller. Bull. Soc. Bot. Belg. **111:** 10–18. 1978.

———. Evolution of male sterility mechanisms in gynodioecious and dioecious species of *Cirsium* (Cynareae-Compositae). Pl. Syst. Evol. **132:** 327–332. 1979.

DERSCHEID, L. A., & R. E. SHULTZ. Achene development of Canada thistle (*Cirsium arvense*) and perennial sowthistle (*Sonchus arvensis*). Weeds **8:** 55–62. 1960.

DETMERS, F. Canada thistle, *Cirsium arvense* Tourn. Ohio Agr. Exp. Sta. Bull. **414:** 1–45. 1927.

DEWEY L. H. Canada thistle (*Carduus arvensis* (L.) Robs.). U. S. Dep. Agr. Bot. Circ. **27:** 1–14. Revised ed. June, 1901.*

DEWOLF, G. P. The stemless thistle, *Cirsium acaule*. Baileya **5**(3): 118, 119. 1957.

DITTRICH, M. Anatomishe Untersuchungen an den Früchten von *Carthamus* L. und *Carduncellus* Adans. Candollea **24:** 263–277. 1969.

DRUCE, G. C. The abridgement of Miller's Gardeners Dictionary of 1754. Rep. Bot. Exchange Club Brit. Isl. **3:** 426–436. 1914.

DUBY, J. E. Aug. Pyrami de Candolle Botanicon gallicum. ed. 2. 1828. Paris. [Source of sect. *Epitrachys* DC.]

DUTTA, C. P., L. P. K. RAY, & D. N. ROY. Taraxasterol, & its derivatives from *Cirsium arvense*. Phytochemistry **11:** 2267–2269. 1972.

FERNALD, M. L. Minor transfers and forms in *Cirsium*. Rhodora **45:** 353–354. 1943a.

———. Eastern extension of *Cirsium Flodmani*. *Ibid.* 356. 1943b.

FORSYTH, S. F., & A. K. WATSON. Predispersal seed predation of Canada thistle. Canad. Entomol. **117:** 1075–1081. 1985.

FRANKTON, C., & R. J. MOORE. Cytotaxonomy, phylogeny and Canadian distribution of *Cirsium undulatum* and *Cirsium Flodmanii*. Canad. Jour. Bot. **39:** 21–33. 1961. [Includes distribution maps.]

——— & ———. Cytotaxonomy of *Cirsium muticum, Cirsium discolor,* and *Cirsium altissimum*. *Ibid.* **41:** 73–84. 1963.

GLYZIN, V. I., V. L. SHELYUTO, A. V. PATUDIN, & N. T. BUBON. Mater S'ezda. Farm. B. SSR. **3:** 153–156. 1977. I. F. URVANTSEV, ed., Minsk. Gos. Med. Inst. USSR.* [Of 62 *Cirsium* spp. almost all contained apigenin, which was found only in inflorescences of some spp. Cynaroside found in infl. of 17 spp., pectolinarin found in 19 spp. (infl., & leaves), linarin in 46 spp., and luteolin in 44 spp.]

GODFREY, R. K. Studies in the Compositae of North Carolina III. An enumeration of noteworthy distribution records. Jour. Elisha Mitchell Sci. Soc. **66:** 186–194. 1950. [*C. carolinianum, C. Smallii.*]

——— & J. W. WOOTEN. Aquatic and wetland plants of southeastern United States. Dicotyledons. x + 933 pp. Athens, Georgia. 1979. [*Cirsium,* 877–881; includes *C. Lecontei, C. Nuttallii, C. virginianum, C. muticum,* and an excellent account of the *C. horridulum* complex.]

GRAY, A. A synopsis of the North American thistles. Proc. Am. Acad. **10:** 39–48. 1874. [A treatment of native *Cirsium* species as *Cnicus.*]

GROH, H. The inflorescence of the Canada thistle (*Cnicus arvensis*). Ontario Nat. Sci. Bull. **3:** 41–42. 1907. [Author reported on imperfectly dioecious nature of this species and morphological changes thus brought about, while noting that some plants of this taxon do not produce seed.]

GUYOT, L., & J. GUILLEMAT. Semences et plantules des principales mauvaises herbes. Paris. 1962.*

HAGGAR, R. J., A. K. OSWALD, & W. G. RICHARDSON. A review of the impact and control of creeping thistle (*Cirsium arvense* L.) in grassland. Crop Protect. **5**(1): 73–76. 1986.

HAYDEN, A. Distribution and reproduction of Canada thistle in Iowa. Am. Jour. Bot. **21:** 355–373. 1934.

HELGESON, E. A., & R. KONZAK. Phytotoxic effects of aqueous extracts of field bindweed and of Canada thistle. A preliminary report. N. Dakota Agr. Exp. Sta. Bull. **12:** 71–76. 1950.*

HILL, E. J. The pasture-thistles, east and west. Rhodora **12:** 211–214. 1910.

HODGSON, J. M. Canada thistle (*Cirsium arvense* Scop.) control with cultivation, croppings and chemical sprays. Weeds **6:** 1–11. 1958.

———. Variation in ecotypes of Canada thistle. *Ibid.* **12:** 167–171. 1964.

———. The nature, ecology and control of Canada thistle. U. S. Dep. Agr. Tech. Bull. **1386.** 32 pp. 1968.

HOLUB, J. Brief comments on the 4th volume of Flora Europaea. Preslia **49**(4): 311–327. 1977. [Numerous nomenclatural notes on a variety of Compositae, *Cirsium* and *Centaurea* in particular; none of the former of concern for the southeastern United States.]

HOWELL, J. T. Sertulum Greeneanum. III. Studies in *Cirsium*. Am. Midl. Nat. **30:** 29–39. 1943.

———. Studies in *Cirsium*. II. Leafl. West. Bot. **9**(1): 9–15. 1959a. [Nomenclature and concepts of several species from the western United States.]

———. Distributional data on weedy thistles in western North America. *Ibid.* **9**(2): 17–29. 1959b. [Species from 9 genera keyed and representative specimens noted, along with earliest record known to the author from the western United States.]

HSI, Y. T. Taxonomy, distribution and relationships of the species of *Cirsium* belonging to the series *Undulata*. Ph.D. thesis, Univ. Minnesota. Univ. Microfilms, Ann Arbor, Michigan.* [Also, Diss. Abstr. **21**(8): 2085–2086. 1961.*]

HUNTER, J. H. Integrated approach to Canada thistle control. Pp. 8–12 *in* 1984 Manitoba Weed Fair. Jan. 1984. Brandon and Winnipeg, Manitoba. 66 pp.*

———, A. I. HSIAO, & G. I. MCINTYRE. Some effects of humidity on the growth and development of *Cirsium arvense*. Bot. Gaz. **146:** 524–530. 1985.

JEFFREY, C. Notes on Compositae: III. The Cynareae in tropical Africa. Kew Bull. **22:** 107–140. 1968.

JONES, S. B., JR. Chromosome numbers in southeastern United States Compositae. I. Bull. Torrey Bot. Club **95:** 393–395. 1968. [*Cirsium virginianum* (as *Carduus virginianus* L.) reported as $n = 11$.]

———. Chromosome numbers in the Compositae. *Ibid.* **97:** 168–174. 1970. [*Cirsium carolinianum*, $n = 11$.]

JONG, T. J. DE, & P. G. KLINKHAMER. The negative effects of litter of parent plants of *Cirsium vulgare* on their offspring; autotoxicity or immobilization. Oecologia **65:** 153–160. 1985. [Under conditions of nutrient deficiency and high population density, immobilization of nitrogen by microorganisms found in *C. vulgare* litter may influence plant growth. This hypothesis differs from those that attribute allelopathic activity to *C. arvense*; see STACHEN & ZIMDAHL.]

KAY, Q. O. N. Hermaphrodites and subhermaphrodites in a reputedly dioecious plant, *Cirsium arvense* (L.) Scop. New Phytol. **100:** 457–472. 1985.

KITAMURA, S. Compositae Japonicae. I. Mem. Coll. Sci. Kyoto Imp. Univ. B. **2:** 87–387. 1937. [Subtribe Carduinae, 31–212; *Cirsium*, 33–134, ca. 90 species in 3 sections (*Megalocephala* Kitamura, *Pseudo-Eriolepis* Nakai, *Onotrophe*).]

KOCH, W. D. Synopsis Flora Germanicae et Helveticae. lx + 844 pp. Francofurti ad Moenum. 1837. [Early treatment of sections of *Cirsium*.]

KRASNIKOV, A. A. Chromosome numbers in some representatives of the family Asteraceae from Siberia USSR. Bot. Zhur. Leningrad **70**(12): 1702–1703. 1985.

KUMAR, V., & D. E. G. IRVINE. Germination of seeds of *Cirsium arvense* (L.) Scop. Weed Res.**11:** 200–203. 1971. [Germination is increased with exposure to light, higher temperatures, and pre-chilling.]

LADYGINA, E. YA. Anatomical and histochemical study of the leaves of *Cirsium setosum* (Willd.) Mb. (In Russian.) Farmatsiya Moscow **29**(6): 17–23. 1980. [Flavonoids mainly located in vacuoles of upper epidermal cells.]

LALONDE, R. G., & J. D. SHORTHOUSE. Growth and development of larvae and galls of

Urophora cardui (Diptera, Tephritidae) on *Cirsium arvense* (Compositae). Oecologia **65:** 161–165. 1985.

LAMP, W. O., & M. K. MCCARTY. Predispersal seed predation of a native thistle, *Cirsium canescens.* Environ. Entomol. **11:** 847–851. 1982.

LEEUWEN, B. H. VAN. Influences of micro-organisms on the germination of the monocarpic *Cirsium vulgare* in relation to disturbance. Oecologia **48:** 112–115. 1981a.

———. The role of pollination in the population biology of the monocarpic species *Cirsium palustre* and *Cirsium vulgare. Ibid.* **51:** 28–32. 1981b.

———. The consequences of predation in the biology of the monocarpic species *Cirsium palustre* and *Cirsium vulgare. Ibid.* **58:** 178–187. 1983.

LEWIS, W. H., H. L. STRIPLING, & R. G. ROSS. Chromosome numbers for angiosperms of the southern United States and Mexico. Rhodora **64:** 147–161. 1962. [*C. horridulum,* 156, $2n = 34$.]

LLOYD, D. G., & A. J. MYALL. Sexual dimorphism in *Cirsium arvense* (L.) Scop. Ann. Bot. II. **40:** 115–123. 1976.

LONG, R. W. Additions and nomenclatural changes in the flora of southern Florida—I. Rhodora **72:** 17–46. 1970. [*Cirsium horridulum* var. *vittatum* (Small) Long, 45.]

——— & O. LAKELA. A flora of tropical Florida. xvii + 962 pp. Coral Gables, Florida. 1971. [*Cirsium horridulum* var. *horridulum* and var. *vittatum, C. Nuttallii,* the only representatives of Cynareae.]

LÖVE, A., & D. LÖVE. *In:* IOPB chromosome number reports LXXV. Taxon **31:** 344–360. 1982. [*Cirsium altissimum,* $2n = 20$; *C. Drummondii,* $2n = 34$; *C. Flodmanii,* $2n = 22$; *C. muticum,* $2n = 20$; *C. undulatum,* $2n = 26$.]

LOVELESS, M. D., & J. L. HAMRICK. Genetic organization and evolutionary history in two North American species of *Cirsium.* Evolution **42:** 254–265. 1988.

MCCALLISTER, R. S., & L. C. HADERLIE. Seasonal variations in Canada thistle (*Cirsium arvense*) root bud growth and root carbohydrate reserves. Weed Sci. **33**(1): 44–49. 1985. [Root-bud growth highest during late fall and winter months following death of aerial shoots; no obvious seasonal patterns in presence of root buds or their ability to elongate at different times of the year.]

MCCARTY, M. K., C. J. SCIFRES, & L. R. ROBINSON. A descriptive guide for major Nebraska thistles. Nebraska Agr. Exp. Sta. Bull. **493.** 24 pp. 1967. [Chiefly *Carduus* and *Cirsium.*]

MCGOWAN, S. G., & J. W. WALLACE. Flavonoids and phenolic acids from *Cirsium lanceolatum.* Phytochemistry **11:** 1503, 1504. 1972.

MEEHAN, T. *Cirsium discolor.* Meehan's Monthly **6:** 161. 1896.

MEINHEIT, K. Der Anatomische Bau des Stengels bei den Compositae Cynareae. Diss. Phil. Fak. Univ. Göttingen. 1907.*

MERRILL, W. A. *Cirsium Smallii* Britton. Quart. Jour. Fla. Acad. Sci. **12:** 65, 66. 1949.

MOORE, R. J., & C. FRANKTON. Cytotaxonomic studies in the tribe Cynareae (Compositae). Canad. Jour. Bot. **40:** 281–293. 1962a.

——— & ———. Cytotaxonomy and Canadian distribution of *Cirsium edule* and *Cirsium brevistylum. Ibid.* **40:** 1187–1196. *maps.* 1962b.

——— & ———. Cytotaxonomy of *Cirsium Hookerianum* and related species. *Ibid.* **43:** 597–613. 1965.

——— & ———. An evaluation of the status of *Cirsium pumilum* and *Cirsium Hillii. Ibid.* **44:** 581–595. 1966.

——— & ———. Cytotaxonomy of foliose thistles (*Cirsium* spp. aff. *C. foliosum*) of western North America. *Ibid.* **45:** 1733–1749. 1967.

——— & ———. Cytotaxonomy of some *Cirsium* species of the eastern United States with a key to eastern species. *Ibid.* **47:** 1257–1275. 1969.

MORTON, J. K. A cytological study of the Compositae (excluding *Hieracium* and *Taraxacum*) of the British Isles. Watsonia **11:** 211–223. 1977.

NELSON, A., & J. B. MACBRIDE. A teratological thistle. Am. Bot. **20:** 136, 137. 1914. [Description of a fasciated specimen of *C. Drummondii.*]

Ownbey, G. B. Natural hybridization in the genus *Cirsium*—I. *C. discolor* (Muhl. ex Willd.) Spreng. × *C. muticum* Michx. Bull. Torrey Bot. Club **78:** 233–253. 1951.

———. Natural hybridization in the genus *Cirsium*—II. *C. altissimum* × *C. discolor.* Michigan Bot. **1:** 87–97. 1964.

———. Nuttall's Great Plains species of *Cirsium*: *C. undulatum* and *C. canescens.* Rhodora **54:** 29–35. 1952.

——— & Y. T. Hsi. Chromosome numbers in some North American species of the genus *Cirsium.* II. Western United States. Madroño **20:** 225–228. 1970.

——— & W. A. Olson. Cytotaxonomic notes on the species of *Cirsium* native to the southeastern United States. Rhodora **71:** 285–296. 1969.

———, P. H. Raven, & D. W. Kyhos. Chromosome numbers in some North American species of the genus *Cirsium.* III. Western United States, Mexico and Guatemala. Brittonia **27:** 297–304. 1975.

Pammel, L. H. The thistles of Iowa, with notes on a few other species. Proc. Iowa Acad. Sci. **8:** 214–239. 1901.

Pavone, P., C. M. Terrasi, & A. Zizza. *In:* Chromosome number reports LXXII. Taxon **30:** 695, 696. 1981.

Petrak, F. Die mexikanischen und zentral-amerikanischen Arten der Gattung *Cirsium.* Beih. Bot. Centralbl. **27:** 207–255. 1910.

———. Beiträge zur Kenntnis der mexikanischen und zentral-amerikanischen Cirsien. Bot. Tidsskr. **31:** 57–72. 1911.

———. Die nordamerikanischen Arten der Gattung *Cirsium.* Beih. Bot. Centralbl. **35:** 223–567. 1917.

———. Über einige Arten und Bastarde der Gattung *Cirsium.* Mitt. Thur. Bot. Ges. **2:** 13–41. 1960.

———. *Cirsium. In:* K. H. Rechinger, ed. Fl. Iran. **139a:** 231–280. 1979.

Piatak, D. M., & L. S. Eichmeier. Plant investigations, II. Hexane extract of *Cirsium arvense.* Trans. Illinois State Acad. Sci. **64:** 300. 1971.*

Pinkava, D. J., & D. Keil. Chromosome counts of Compositae from the United States and Mexico. Am. Jour. Bot. **64:** 680–686. 1977. [Four species of *Cirsium* reported: *C. arizonicum,* $2n = 15_{\mathrm{II}}$; *C. coloradense,* $2n = 17_{\mathrm{II}}$; *C. Flodmanii,* $2n = 12_{\mathrm{II}}$; *C. undulatum,* $2n = 12_{\mathrm{II}}$ and $2n = 13_{\mathrm{II}}$).]

Poddubnaja-Arnoldi, W. Ein Versuch der Anwendung der embryologischen Methode bei der Lösung einiger systematischer Fragen. I. Vergleichende embroyologisch-zytologische Untersuchungen über die Gruppe Cynareae, Fam. Compositae. Beih. Bot. Centralbl. **48:** 141–237. 1931.

Putnam, B. L. A white form of *Carduus arvensis.* Asa Gray Bull. **7:** 37. 1899. [*Cirsium arvense.*]

Robinson, B. L. Notes on the genus *Cirsium.* Rhodora **13:** 238–240. 1911.

Rostovtseva, T. S. Chromosome numbers of some species of the family Asteraceae. Biol. Zhur. Leningrad **64:** 582–589. 1979. [*Cirsium incanum* (S. G. Gmel.) Fisch. ex Bieb., $2n = 28$; *Carduus crispus,* $2n = 18$.]

———. Chromosome numbers of some species of the family Asteraceae 2. *Ibid.* **68:** 660–664. 1983. [*Arctium Lappa* L., $2n = 36$; *Cirsium heterophyllum* (L.) Hill, $n = 17$.]

Rydberg, P. A. Studies on the Rocky Mountain flora—XXIV. Bull. Torrey Bot. Club **37:** 541–557. 1910. [Notes on numerous *Cirsium* taxa (as *Carduus*), particularly hybrids; four new species of *Cirsium* described as *Carduus.*]

———. Flora of the Rocky Mts. and Adjacent Plains. xii + 1110 pp. Published by the author, New York. 1917.

———. Flora of the Prairies and Plains of Central North America. vii + 969 pp. Published by the New York Botanical Garden, New York. 1932. [Cynareae, 879–886; *Cirsium,* 879–883, 18 spp. treated.]

Scopoli, J. A. Methodus Plantarum. 28 pp. Vienna. 1754. [*Cirsium,* 19, listed with *Carduus* and *Arctium* (as *Lappa*) under Classis Flosculosae.]

———. Flora Carniolica. xxii + 607 pp. Vienna. 1760. [*Cirsium* treated with description; seven species listed without binomials.]

———. Flora Carniolica. ed. 2. lxxii + 448 pp. Vienna. 1772. [*Cirsium,* 123; 15 species described and given binomials.]

Scrugli, A., E. Boccieri, & C. Del Prete. Chromosome numbers for the Italian flora, part 331–365. Inf. Bot. Ital. **9**(2): 116–140. 1977. [*Cirsium vulgare* ssp. *sylvaticum* (Tausch) Dostal, $2n = 68$; tetraploid of $x = 17$.]

Shelyuto, V. L., V. I. Glyzin, & A. I. Ban'kovskii. Flavonoids of *Cirsium arvense.* Chem. Nat. Compounds **6**(3): 366. 1970.*

———, ———, ———, & N. T. Bubon. Flavonoids of *Cirsium oleraceum* flowers. Khim. Prir. Soedin. **7**: 371 ff. 1971.*

———, ———, & N. T. Bubon. Flavonoids of *Cirsium palustre. Ibid.* **2**: 241 ff. 1972a.*

———, ———, & ———. 3-O-Methylkaempherol from *Cirsium arvense. Ibid.* **7**: 371 ff. 1972b.*

Shih, C. Notulae de plantis tribus Cynarearum familiae Compositarum Sinicae. II. (In Chinese; English summary.) Acta Phytotax. Sinica **22**: 445–455. 1984. [Forty-nine species of *Cirsium* reported for China (9 newly described, 4 new records reported) divided among 8 sections (3 newly described).]

Shinners, L. H. Notes on Texas Compositae—I. Field & Lab. **17**: 23–30. 1949. [*Cirsium terrae-nigrae* Shinners described.]

———. New names and records for Texas Compositae. Sida **1**: 373–379. 1964. [*Cirsium terrae-nigrae* Shinners placed in synonymy under *C. Engelmannii.*]

Štepa, I. S. Morphology of pollen of the genus *Cirsium* Mill. and of close genera of the tribe Cynareae (Compositae). (In Russian.) Trudy Tbilis. Bot. Inst. Acad. Nauk SSSR. **21**: 81–126. 1961.

Skalinska, M., J. Malecka, R. Izmailow, *et al.* Further studies in chromosome numbers of Polish angiosperms. XII. Acta Biol. Cracov. Bot. **19**: 107–148. 1974.

Small, J. K. Additions to the flora of subtropical Florida. Bull. New York Bot. Gard. **3**: 419–440. 1905. [Description of *Carduus vittatus* Small (= *Cirsium vittatum* (Small) Small).]

———. Flora of Miami. xii + 206 pp. Published by the author. New York. 1913. [Key to *Cirsium vittatum* (Small) Small, *C. pinetorum* (Small) Small, and *C. horridulum,* 199.]

Smith, T. On certain species of *Carduus* and *Cnicus* which appear to be dioecious. Trans. Linn. Soc. London **13**: 592–603. 1822.

Stachen, W. J., & R. L. Zimdahl. Allelopathic activity of Canada thistle (*Cirsium arvense*) in Colorado. Weed Sci. **28**: 83–86. 1980.

Stoutamire, W. P., & J. H. Beaman. Chromosome studies of Mexican alpine plants. Brittonia **12**: 226–230. 1960. [*Cirsium cernuum* and *C. subcoriaceum,* both as $n = 17$.]

Strid, A., & R. Franzen. *In:* Chromosome number reports LXXII. Taxon **30**: 829–842. 1981. [Three *Cirsium* species from Greece reported to be $2n = 34$; *C. vulgare* confirmed as $2n = 68$.]

Thieret, J. W. Twenty-five species of vascular plants new to Louisiana. Proc. Louisiana Acad. Sci. **32**: 78–82. 1969. [*C. terrae-nigrae* Shinners new to Louisiana: Caddo Parish, 2 mi. SE of Mooringsport, *Thieret 25999* det. G. B. Ownbey, who was reported to be revising N. American *Cirsium.* Cf. Shinners, 1964.]

Tonyan, T. R. Caryological data on species of *Cirsium* Mill. growing in Armenia. (In Russian.) Biol. Zhur. Armenii. SSR. **34**(7): 769–772. 1981. [*C. arvense, C. incanum* (S. G. Gmel.) Fisch. ex Bieb., and *C. echinus* (Bieb.) Hand.-Mazz. reported as $2n = 34$.]

———. New chromosome numbers of the species of *Cirsium* in Armenia. (In Russian.) Ucen. Zap. Erevan Univ. **3:** 115–120. 1982.*

Toumey, J. W. Fasciation in *Cnicus lanceolatus.* Bot. Gaz. **16:** 236. 1891. [*C. vulgare.*]

Turner, B. L., W. L. Ellison, & R. M. King. Chromosome numbers in the Compositae. IV. North American species, with phyletic interpretations. Am. Jour. Bot. **48:** 216–223. 1961. [*C. horridulum,* $n = 16$.]

Turner, S. K., P. K. Fay, E. L. Sharp, & D. C. Sands. Resistance of Canada thistle, *Cirsium arvense,* ecotypes to a rust pathogen, *Puccinia obtegens.* Weed Sci. **29**(6): 623, 624. 1981.

Van Loon, J. C., & H. De Jong. *In:* IOPB chromosome number reports LIX. Taxon **27:** 53–61. 1978. [*C. arvense,* $2n = 34$; *C. palustre,* $2n = 34$.]

Wallace, J. W. Tricin-5-O-glucoside and other flavonoids of *Cirsium arvense.* Phytochemistry **13:** 2320, 2321. 1974. [Quercetin-3-O-digalactoside and quercetin-3-O-rhamnoglucoside found to be major constituents; cirsimaritin-4′-O-rutinoside reported as a minor constituent.]

——— & B. A. Bohm. Cirsimaritin-4′-O-rutinoside, a new flavone glucoside from *Cirsium brevistylum.* Phytochemistry **10:** 452–454. 1971. [Compound not found in *C. edule, C. undulatum, C. vulgare,* or *C. arvense*; bibliography includes citations for early work on several Japanese taxa.]

Watson, A. K., R. Beauregard, & W. Keogh. Biological control of Canada thistle in Quebec. Canada Thistle Symp. Agr. Canada, March, 1980, Regina, Saskatchewan. 200 pp. 1980.

Wells, H. Hybridization and genetic recombination of *Cirsium californicum* and *Cirsium occidentale* (Asteraceae: Carduaceae). Madroño **30:** 12–30. 1983.

Werner, K. *Cirsium. In:* T. G. Tutin *et al.,* eds., Fl. Europaea **4:** 232–242. 1976.

Willaman, J. J., & B. G. Schubert. Alkaloid-bearing plants and their contained alkaloids. U. S. Dep. Agr. Tech. Bull. **1234.** 287 pp. 1961. [Unnamed alkaloids reported in *Cirsium arvense* and *C. setigerum* Ledeb., 68.]

——— & H. L. Li. Alkaloid-bearing plants and their contained alkaloids. Lloydia **33** (Supplement): vii + 286 pp. 1970.

Williams, J. T. Variation in the germination of several *Cirsium* species. Trop. Ecol. **7:** 1–7. 1966. [Five species, including *C. arvense* and *C. vulgare,* studied. Germination rate of *C. arvense* achenes found to be quite variable, with a range of 34.3 to 66.3 percent. Range for *C. vulgare* was between 26.2 and 41.6 percent. Common parasitization of *Cirsium* achenes by beetle larvae, fruit flies, and rusts also noted.]

Wilson, M. F., P. K. Anderson, & P. A. Thomas. Bracteal exudates in two *Cirsium* species as possible deterrents to insect consumers of seeds, *Cirsium discolor, Cirsium Flodmani.* Am. Midl. Nat. **110:** 212–214. 1983.

Wilson, R. G., & M. K. McCarty. Germination and seedling and rosette development of Flodman thistle (*Cirsium Flodmanii*). Weed Sci. **32:** 768–773. 1984. [Light important in seed germination; greatest seedling emergence occurred when seeds were planted on soil surface.]

Wu, T. S., C. S. Kuoh, & S. I. Jen. Constituents of Formosan folk medicine. VIII. Flavonoids of the leaves of *Cirsium albescens, C. japonicum* var. *australe, C. Kawakamii* f. *variegatum* and *C. Hosogawa.* T'ai-wan Yao Tsa Chih. **32**(2): 88–90. 1981. [Linarin, a flavone glycoside, was isolated from leaves of all; *C. Hosogawa* leaves also yielded luteolin, luteolin-7-glucoside, and linarin.]

Wynn-Williams, M. Observations upon the seeds and germination of some thistle species. Int. Seed Test. Assoc. **6:** 4–10. 1934.*

Zilke, S., & L. A. Derscheid. Factors affecting germination of Canada thistle and perennial sowthistle seeds. N. Cent. Weed Control Conf. Proc. **14:** 42, 43. 1957.*

2. **Carduus** Linnaeus, Sp. Pl. **2:** 820. 1753; Gen. Pl. ed. 5. 358. 1754.

Biennial [annual or perennial] herbs. Stems to ca. 2 m tall, fibrous, glabrous to arachnoid-tomentose, spiny winged, wings triangular to palmate, occasionally with an apical spine 1–5 mm long. Leaves sessile to more often petiolate; blades lanceolate to oblanceolate, deeply lobed to 2-pinnatisect [subentire], to ca. 25 cm × 10 cm, the upper surface glabrescent to sparsely [densely] pubescent, occasionally punctate glandular, the abaxial surface glabrous to densely arachnoid-villous and often glandular, hairs crispate or sinuate, multicellular, glands capitate or punctate; margins often with an apical spine to 5 mm [exceeding 10 mm]. Capitula homogamous, discoid, subglobose [globose], 1.5–2.5 [8] cm wide, sessile or in clusters of 2–4 [10 or more] on narrowly winged peduncles. Involucre ovoid, bracts imbricate in 5–8 [10] series, linear-lanceolate to oblanceolate, acute to acuminate, spine tipped or sharply mucronate, spreading or reflexed [adpressed], glabrous to densely pubescent, occasionally minutely glandular; margins entire, scabrous or ciliate; outer bracts long-acuminate to acute, inner bracts longer than middle, acute [obtuse], shortly contracted to a spinule, obscurely 1–5 veined, occasionally contracted slightly below middle. Receptacle densely setose. Flowers perfect, actinomorphic or zygomorphic. Corolla purple, lavender, [pink or white], tube narrow, throat short and unequally divided by sinuses of corolla lobes with 2 sinuses deeper than the others, lobes linear, elongate (ca. 4–5 mm long), glabrous or sparsely glandular. Staminal filaments sparsely to densely pubescent, anthers white, sagittate, with slender, entire or lacerate basal appendages, apical appendage acute, small. Styles smooth below a distinct collar of hairs at base of the relatively short, papillose, scarcely divergent, narrowly truncate to acute branches. Achenes basifixed, 3–5 mm long, somewhat compressed, glabrous, smooth [rugulose when dried] with 5–10 ribs and a distinct annular margin at apex. Pappus bristles in several rows, connate at base, unequal, inner setae longer than outer, white, not plumose, smooth to barbellate. LECTOTYPE SPECIES: *Carduus nutans* L.; see Britton & Brown, Illus. Fl. No. U. S. Canad. ed. 2. **3:** 554. 1913. (Name the ancient Latin one.)—PLUMELESS THISTLE.

A genus of 91 species, according to Kazmi (1963, 1964), distributed in Eurasia and northern Africa. Two introduced and naturalized species occur in the southeastern United States.

As established by Linnaeus, *Carduus* was composed of 23 species, several of which were later placed in *Cirsium* by Scopoli (1772) (see discussion under *Cirsium*). While the strength of the characters used to distinguish these genera (pappus of smooth or barbellate setae vs. pappus of plumose setae) has been questioned (Correll & Johnston; Willis) most workers have treated *Cirsium* and *Carduus* separately. Recently, though, Ahles in Radford *et al.* included in *Carduus* 13 taxa that are considered in this paper to be members of *Cirsium.*

The 91 species recognized by Kazmi (1963, 1964) were placed in two subgenera (CARDUUS, AFROCARDUUS Kazmi) of Eurasian and African distribution. He later (1964) proposed a third subgenus (ALFREDIA (Cass.) Kazmi) based on characters of the corolla lobes, staminal filaments, and pappus. Subgenus AFROCARDUUS was delimited by hooked corolla lobe apices, glabrous or sometimes tuberculate filaments, and opaque achenes. AFROCARDUUS is comprised of ca. 21 African species that are placed among sections ACAULON Kazmi (7 spp.), AFROCARDUUS Kazmi (8 spp.), and PINNATISQUAMA Kazmi (6 spp.). For subg. ALFREDIA, represented by species from Afghanistan, western Pakistan, eastern Russia, Mongolia, Tibet, and China, Kazmi (1964) proposed sections ALFREDIA, PTEROCAULON, and APTERON but did not give a treatment of species. Moore & Frankton (1962) reported that sect. ALFREDIA contains six species distinguished by their yellow flowers.

Subgenus CARDUUS (70 spp.) (Kazmi, 1964) is distinguished by smooth corolla lobes, villous staminal filaments, and pappus usually of whitish or, rarely, stramineous bristles. The distribution of this group extends from the Mediterranean region to northern Europe with several widespread species that are now encountered in many areas of the United States.

The two species *Carduus acanthoides* L. and *C. nutans* L., musk-thistle, known to occur in the Southeast are members of subg. CARDUUS. Both belong to the type section, one of two (CARDUUS, LEPTOCEPHALI Reichenb. f.) recognized in the group (Kazmi, 1964; Franco, 1976). *Carduus crispus* L., a species sparingly introduced in the United States, and also a member of sect. CARDUUS, has not been reported in the Southeast, but eventually may be encountered in the northern parts of the area along roadsides or in disturbed areas (Johnson, 1974).

Both *Carduus nutans* and *C. acanthoides* are widely established in the United States along roadsides and in pastures and disturbed areas. Hensley observed that both species thrive in areas of high-calcium limestone deposited at very shallow depths. *Carduus acanthoides* does not extend south of a few localized occurrences in western North Carolina (Radford *et al.*) and, perhaps, Tennessee, yet *C. nutans* has been collected as far south as Georgia, Mississippi, and Louisiana. Both species are monocarpic, outcrossing (Smyth & Hamrick) biennials that can be differentiated by capitulum and involucre size and the orientation of the capitula (heads nodding in *C. nutans* vs. upright or erect in *C. acanthoides*). Moore & Frankton (1974) recognized three subspecies of *C. nutans* in Canada, and Kazmi (1964) added a fourth from northern Europe. Two subspecies of *C. acanthoides* were described by Kazmi (1964).

Cytological studies have reported chromosome numbers of $2n = 16$ ($n = 8$) for *C. nutans* (Poddubnaja-Arnoldi; Górecka; Löve & Löve, 1944; Moore & Frankton, 1962; Devesa; Van Loon & De Jong; Van Loon & Kieft; Van Loon & Snelders) and $2n = 22$ for *C. acanthoides* (Górecka; Löve & Löve, 1944; Moore & Frankton, 1962; Poddubnaja-Arnoldi; Van Loon & Kieft). Mehra and colleagues and Mehra & Remanandan have reported chromosome numbers of $2n = 40$ ($n = 20$) for *C. nutans* with laggards and bridges mildly disturbing meiosis. The chromosome number for *C. crispus* has consistently been reported as $2n = 18$ (Arano; Górecka; Löve & Löve, 1944; Poddubnaja-Arnoldi; Probatova & Sokolovskaya; Rostovtseva).

Moore & Frankton (1962) suggested a base chromosome number of 8 or 11 for the genus. The lower numbers were thought to result from reduction brought about by fragmentation and fusion. Polyploids appear to be rare in *Carduus*, with $2n = 54$ first reported for *C. tenuiflorus* Curt. and *C. pycnocephalus* L. by

Moore & Frankton (1962). They speculated that these species are hexaploids of the base number 9 formed by hybridization between a diploid and a tetraploid species followed by doubling of the chromosome number of the hybrid.

Hybridization is commonly reported in *Carduus* (Arènes, 1949; Briquet, 1931; Devesa; Kazmi, 1964; McCarty; Moore & Mulligan, 1956). Kazmi (1964) listed crosses between *C. acanthoides* and 14 other species and between *C. nutans* and four others.

Moore & Mulligan's (1959) study of hybridization between *C. nutans* and *C. acanthoides* (= *C.* × *orthocephalus* Wallr.) showed that several morphologically intermediate plants had chromosome numbers ($2n = 17, 18, 19, 21$) intermediate between those of the parental species. They also noted a strong correlation between morphology and chromosome number (i.e., the more closely a hybrid approached the morphology of one of the parental types the more likely it was to have a chromosome number either close to or the same as that parent). A few hybrid plants had chromosome numbers of $2n = 16$, but the majority of the hybrids had chromosome numbers of $2n = 22$, which led Moore & Mulligan to hypothesize that backcrossing to both parents had occurred to produce the chromosome numbers of the parental stock. Of the carpellate parents with a known chromosome number of $2n = 22$, 23 of the 24 hybrid progeny examined had $2n = 22$.

Wagner reported the alkaloids acanthoine and acanthoidine for *Carduus acanthoides* and referred readers to Bohlmann *et al.* for a list of polyacetylenes. No sesquiterpene lactones were noted by Seaman for *Carduus,* but Abdel-Salam isolated an unusual triterpene ester from *C. getulus* Pomel. Amer and colleagues' report of flavonoids from *C. pycnocephalus* appears to be one of the few reports of flavonoids isolated from *Carduus.*

There are no economically important members of this group.

REFERENCES:

Under tribal references see ARANO; BOBROV & CZEREPANOV; BOHLMANN *et al.*; BRIQUET, 1931; CORRELL & JOHNSTON; CRONQUIST, 1980; GOLDBLATT, 1981, 1984, 1985; HEGI, 1928–29, 1987; JOHNSON, 1974; LÖVE & LÖVE, 1944; MABBERLEY; MACROBERTS; MEHRA *et al.*; MEHRA & REMANANDAN; D. M. MOORE; MOORE & FRANKTON, 1962, 1974; PODDUBNAJA-ARNOLDI; RADFORD *et al.*; RICKETT; SMALL, 1933; SCOPOLI, 1772; E. B. SMITH; WAGNER; WILLAMAN & SCHUBERT; WILLAMAN & LI; and WILLIS.

ABDEL-SALAM, N. A., I. MORELLI, & S. CATALANO. An unusual triterpene ester in a compositaceous plant, *Carduus getulus.* Int. Jour. Crude Drug Res. **21**: 79–80. 1983.*

AMER, M. M. A., O. M. SALAMA, & A. A. OMAR. Flavonoids of *Carduus pycnocephalus.* Fitoterapia **1985**(1): 61. 1985.

ARÈNES, J. Contribution à l étude du genre *Carduus.* Mém. Mus. Natl. Hist. Nat. Paris. II. **24**: 183–255. 1949.

———. Sur la systématique de quelques *Carduus.* Not. Syst. Paris **15**(4): 390–410. 1959.

BATRA, S. W. T. Insects and fungi associated with *Carduus* thistles (Compositae). U. S. Dep. Agr. Sci. & Educat. Admin. 100 pp. Washington, D. C. 1981.*

CORY, V. L. Six thistles introduced into Texas. Madroño **5**: 200–202. 1940. [*C. pycnocephalus, C. nutans.*]

DAVIS, P. H. *Carduus.* Notes Bot. Gard. Edinburgh **33**: 413. 1975.

———. *Carduus. In:* P. H. DAVIS, ed. Fl. Turkey **5**: 420–438. 1975.

DEVESA, J. A. Contribución al estudio cariologico del genero *Carduus* en la peninsula Iberica. Lagascalia **10:** 65–81. 1981. [Chromosome numbers of 22 taxa of *Carduus*; base numbers of 8, 9, 10, & 11 reported; *C. nutans* reported as $n = 8$, $2n = 16$; *C. tenuiflorus* reported as $2n = 54$, presumably an allopolyploid from $x = 8$ and $x = 11$ ancestors.]

FRANCO, J. do AMARAL. *Carduus. In:* T. G. TUTIN *et al.*, eds., Fl. Europaea **4:** 220–232. 1976. (Key by M. L. ROCHA AFONSO.)

FRIES, R. E. Revision der tropisch-afrikanischen *Carduus*-Arten. Acta Horti Berg. **8:** 11–38. 1923. [Twenty-two species of *Carduus* of which 14 are newly described.]

GORECKA, A. Cytological studies in three species of *Carduus* L. (In Polish; English summary.) Acta Soc. Bot. Polon. **25:** 719–731. 1956.*

GREMAUD, M. An attempt at experimental taxonomy in the *defloratus* group of the genus *Carduus* (Compositae). II. Morphological variation, numerical taxonomy. (In French.) Rev. Cytol. Biol. Veg. Bot. **4:** 111–171. 1981. [Includes illustrations and maps.]

HAMRICK, J. L., & J. M. LEE. Effect of soil surface topography and litter cover on the germination, survival, and growth of musk thistle (*Carduus nutans*). Am. Jour. Bot. **74:** 451–457. 1984.

HARRIMAN, N. A. *In:* IOPB chromosome number reports XLVIII. Taxon **24:** 367–372. 1975. [*C. acanthoides*, $2n = 22$.]

HENSLEY, M. S. Distribution of *Cirsium* and *Carduus* thistles in Rockingham County, Virginia. [Abstr.] Virginia Jour. Sci. **24:** 140. 1973.

HILL, E. J. *Carduus Hillii* perennial. Pl. World **2:** 127. 1899.

HOWELL, J. T. *Carduus* in California. Leafl. West. Bot. **2:** 212, 213. 1939.

KAZMI, S. M. A. Revision der Gattung *Carduus* (Compositae), I. Mitt. Bot. Staatssamml. München **5:** 139–198. 1963; II. *Ibid.* 279–550. 1964.

KITAMURA, S. Compositae Japonicae. Mem. Coll. Sci. Kyoto Univ. B. **13:** 1–421. 1937. [One species of *Carduus, C. crispus* L., treated, 32, 33.]

KOK, L. T. Status of two European weevils for the biological control of *Carduus* thistles in the U.S.A. [*Rhinocyllus conicus, Ceuthorhynchidius horridus.*] Acta Phytopathol. **16:** 139–142. 1981.*

KUZMANOV, B., & S. GEORGIEVA. *In:* IOPB chromosome number reports LIII. Taxon **25:** 483–500. 1976. [*C. acanthoides*, $2n = 22$.]

LEE, J. M., & J. L. HAMRICK. Demography of two natural populations of musk thistle (*Carduus nutans*). Jour. Ecol. **71:** 923–936. 1983.

MCCARTY, M. K. A nursery study of large-flowered taxa of *Carduus*. Weed Sci. **33:** 664–668. 1985.

———, C. J. SCIFRES, & L. R. ROBINSON. A descriptive guide for major Nebraska thistles. Nebraska Agr. Exp. Sta. **SB 493.** 24 pp. 1967. (U. S. Dep. Agr. cooperating.) [Chiefly *Carduus* and *Cirsium.*]

MESTRE, J. C. Composées-Cynarées; développement de l'embryon chez le *Carduus nutans* L. Compt. Rend. Acad. Sci. Paris **245:** 355–358. 1957.

MOORE, R. J., & G. A. MULLIGAN. Natural hybridization between *Carduus acanthoides* and *Carduus nutans* in Ontario. Canad. Jour. Bot. **34:** 71–85. 1956.

——— & ———. A study of natural hybridization between *Carduus acanthoides* and *Carduus nutans.* Proc. 10th Int. Congr. Genetics, Montreal, 1958. **2:** 193. 1959.

MORTON, J. K. A cytological study of the Compositae (excluding *Hieracium* and *Taraxacum*) of the British Isles. Watsonia **11:** 211–223. 1977.

MULLIGAN, G. A., & C. FRANKTON. The plumeless thistles (*Carduus* spp.) in Canada. Canad. Field Nat. **68:** 31–36. 1954.

——— & R. J. MOORE. Natural selection among hybrids between *Carduus acanthoides* and *C. nutans* in Ontario. Canad. Jour. Bot. **39:** 269–279. *map.* 1961.

MURIN, A., & M. VACHOVA. *In:* Index of chromosome numbers of Slovakian flora. Part 6. Acta Fac. Rerum Nat. Univ. Comenianae Bot. **26:** 1–42. 1978.

OLIVIERI, I. Comparative electrophoretic studies of *Carduus pycnocephalus* L., *Carduus tenuiflorus* Curt. (Asteraceae), and their hybrids. Am. Jour. Bot. **72:** 715–718. 1985.

———, M. SWAN, & P. H. GOUYON. Reproductive system and colonizing strategy of two species of *Carduus* (Compositae). Oecologia **60:** 114–117. 1983.

RECHINGER, K. H. *Carduus. In:* K. H. RECHINGER, ed., Fl. Iran. **139a:** 218–230. 1979.

REES, N. E. Two species of milk thistle (*Carduus* spp.) as hosts of *Rhinocullus conicus.* Weed Sci. **34:** 241–242. 1986.

ROSTOVTSEVA, T. S. Chromosome numbers of some species of the family Asteraceae Dumort. (In Russian.) Bot. Zhur. Leningrad **64:** 582–589. 1979. [*Carduus crispus,* $2n = 18$.]

SMITH, L. M., II, & L. T. KOK. Dispersal of musk thistle (*Carduus nutans*) seeds. Weed Sci. **32:** 120–125. 1984.

SMYTH, C. A., & J. L. HAMRICK. Variation in estimates of outcrossing in musk thistle, *Carduus nutans,* populations. Jour. Hered. **75:** 303–307. 1984.

VACHOVA, M. *In:* Index of chromosome numbers of Slovakian flora. Part 5. Acta Fac. Rerum Nat. Univ. Comenianae Bot. **25:** 1–18. 1976.

VAN LOON, J. C., & H. DE JONG. *In:* IOPB chromosome number reports LIX. Taxon **27:** 53–61. 1978. [*Carduus nutans,* $2n = 16$; *Centaurea maculosa,* $2n = 18$; *Cirsium arvense,* $2n = 34$.]

——— & B. KIEFT. *In:* Chromosome number reports LXVIII. Taxon **29:** 538–542. 1980. [*Carduus nutans,* $2n = 16$; *C. acanthoides,* $2n = 22$.]

——— & H. C. M. SNELDERS. *In:* IOPB chromosome number reports LXV. Taxon **28:** 632–634. 1979. [*C. nutans,* $2n = 16$.]

3. **Silybum** Adanson, Fam. Pl. **2:** 116, 605. 1763, nom. cons.

Annual or biennial herbs. Stems 20–150 cm tall, simple or sparingly branched, robust, glabrous or slightly tomentose, lacking wings. Leaves near base of stem petiolate, upper cauline leaves sessile and auriculate-clasping; blades to 80 cm long and nearly 40 cm wide, broadly lanceolate to oblanceolate, lower leaves deeply but irregularly lobed, upper leaves entire or shallowly lobed, white veined or variegated, glabrescent to puberulent; margins spiny. Capitula 3–6 cm wide, homogamous, discoid, solitary at the ends of branches. Involucre hemispheric to ovoid; bracts imbricate, multiseriate, the outer ones with a broad, firm, spinulose-ciliate base and a coriaceous, subfoliose, strongly reflexed, spine-tipped and basally spine-margined appendage, inner bracts lanceolate, erect and unappendaged. Receptacle flat to slightly convex, densely bristly. Flowers perfect. Corolla slightly zygomorphic, purplish; tube narrow, elongate, glabrous to puberulent, throat short, abruptly expanded, unequally divided by the sinuses of the long, linear, acute lobes. Staminal filaments glabrous, connate below; anthers shortly tailed at base, apical appendage firm, triangular, glabrous. Style smooth below a distinct collar of hairs at base of the elongate, papillose, connate branches. Achenes basifixed, obovoid-oblong, 6–7 mm long, somewhat compressed, glabrous, black or brown with lighter streaks, with a distinct annular rim subtending the pappus. Pappus in several series, outer setae white, minutely barbellate, innermost bristles considerably shorter, capillaceous, basally connate and deciduous as unit. Base chromosome number 17. TYPE SPECIES: *Carduus Marianus* L. = *Silybum Marianum* (L.) Gaertner, type cons. (Name the Latin one for the milk-thistle, from the Greek name *sillybos* or *silybon.*)—MILK-THISTLE.

A genus of two species, *Silybum Marianum* (*Mariana Mariana* (L.) Hill) and *S. eburneum* Coss. & Dur., both native to the Mediterranean area, the former now widespread in North and South America. *Silybum Marianum*, milk-thistle, $2n = 34$, is naturalized locally in many parts of the United States, particularly in drier waste areas, along roadsides, and in disturbed pastures. In the Southeast it is rare and may be little more than a waif locally escaped from cultivation. Small (1933) reported it south to Alabama; Cory listed it west to Texas; yet it was not treated by either Correll & Johnston or Barkley). Johnson (1978) recorded it from Goochland County, Virginia; Thieret (1968) reported it as new to Louisiana, and E. B. Smith (1988) noted it as a local escape from cultivation in three widely separated localities in Arkansas. This species has become a common and troublesome weed in the pampas of Argentina (Mabberly) and in areas with a Mediterranean climate along the Pacific coast of North America (Howell, Munz), where a seed weevil, *Rhinocyllus conicus*, (Hawkes *et al.*, 1972) has been released to control it.

Silybum Marianum was treated as a species of *Carduus* by Linnaeus and was initially given generic status as *Mariana* by Hill. Shortly afterward Adanson proposed the now conserved name *Silybum* for the same taxon. Cassini grouped *Silybum* with *Alfredia* Cass. (= *Carduus* subgenus *Alfredia* (Cass.) Kazmi) and *Echenais* Cass. (treated as *Carduus* by Lessing, *Cnicus* by Bentham) as an unspecified division of the Carduinae. Lessing placed *Silybum* with *Tyrimnus* Cass. and *Galactites* Moench in an unranked division, *Silybeae*, of the subtribe Carduinae, on the basis of their monadelphous filaments, multiseriate pappus, and compressed, glabrous achenes. The same genera were recognized as subtribe *Silybeae* by De Candolle. A detailed study of seed anatomy and morphology led Dittrich (1970, 1977) to group *Silybum* informally with *Carduus, Cirsium*, and *Modestia* Charadze & Tamamshiam, while *Galactites* and *Tyrimnus* were aligned with *Picnomon* Adanson and *Jurinea* Cass.

Silybum is distinguished from *Galactites, Cirsium*, and *Modestia* by its simple or barbellate (not plumose) pappus bristles. It differs from *Tyrimnus* and *Carduus* in its uniseriate pappus and mottled cauline leaves that are markedly different from the reduced leaves that subtend individual heads. In addition, *Silybum* is distinguished from other genera of Cardueae of the Southeast by its connate staminal filaments.

Chromosome counts of $2n = 34$ have been reported for *Silybum Marianum* (Goldblatt, 1981; Heiser & Whittaker; Larsen). Moore & Frankton (1962) found that the chromosomes of *Silybum* are somewhat shorter than those of *Cirsium* but are similar in width and appearance. They also noted that the thickness of the chromosomes and the total amount of chromatin in the nucleus are similar in species of *Silybum, Carduus, Cirsium, Cnicus*, and *Onopordum*.

Wagner reported that flavanones and flavonols were restricted to *Silybum, Centaurea*, and *Carthamus*. Both species of *Silybum* were noted as exceptional for their production of flavonolignans, compounds known from only one other genus, *Hydnocarpus* (Flacourtiaceae). Flavonoids isolated from *Silybum* include silybin, silydianin, silychristin, and silymarin (Wagner *et al.*, 1971; Wagner, 1977; Cappelletti & Caniato, 1983, 1984; Belikov, 1985; Hassan, 1985). The antihepatotoxic activity of the flavonolignans has been of considerable interest for medicinal purposes (Hahn *et al.*; Sharma & Singh; Schrall & Becker; Fiebig & Wagner; Hikino *et al.*; Wagner, 1986). Mabberley noted that the antihepatotoxic qualities of *S. Marianum* have been known since the time of Dioscorides and that they are now known to work as effective antidotes for *Amanita* poisoning, since they are able to displace phalloidin from membrane receptors. In addition, the alkaloids tyramine and histamine have been isolated from *Silybum* (see Wagner, 1977, for references).

REFERENCES:

Under tribal references see BARKLEY, 1986; BOBROV & CZEREPANOV; CORRELL & JOHNSTON; CRONQUIST, 1980; DE CANDOLLE; DITTRICH, 1970, 1977; GAERTNER; GOLDBLATT, 1981; HEGI, 1928–29, 1987; HEISER & WHITTAKER; HOWELL; LARSEN; LAVIALLE; LESSING; MABBERLEY; MACROBERTS; MOORE & FRANKTON, 1962, 1974; Poddubnaja-ARNOLDI; SINGH & PANDEY; SMALL, 1933; E. B. SMITH; WAGNER, 1977; and ZWÖFLER, 1965.

AUSTIN, M. P., R. H. GROVES, L. M. F. FRESCO, & P. E. KAYE. Relative growth of 6 thistle species along a nutrient gradient with multispecies competition. Jour. Ecol. **73:** 667–684. 1985.

BELIKOV, V. V. Determination of the content of flavanol derivatives in the fruits of *Silybum Marianum.* (In Russian.) Rastit. Resur. **21:** 350–358. 1985.

BOLDT, P. E., & L. T. KOK. Bibliography of *Phinocyllus conicus* Froel. (Coleoptera: Curculionidae), an introduced weevil for the biological control of *Carduus* and *Silybum* thistles. Bull. Entomol. Soc. Am. **28:** 355–358. 1982.*

CAPPELLETTI, E. M., & R. CANIATO. Chemical characterization of wild Italian populations of *Silybum Marianum* (L.) Gaertn. Plant-Med-Phytother. **17:** 209–214. 1983. [Flavonoid content and the ratios of flavolignan isomers silybin, silydianin and silychristin investigated from populations in central and southern Italy.]

——— & ———. Silymarin localization in the fruit and seed of *Silybum Marianum.* Herba Hung. **23:** 53–66. 1984. [Silymarin (2,4-dinitrophenyl-hydrazine) localized in pericarp, seed integument, and endosperm; 2, 4-DNPH localized in subepidermal and membraniform layers of pericarp. All layers of seed integument contain flavolignans; 2,4 DNPH and flavolignans were not found in cotyledons as suggested by LANGHAMMER. Flavolignans may play an ecological role as allelopathic agents through flavolignan-induced IAA oxydase inhibition in other plants; also report on a subepidermic layer of thin-walled cells, some devoid of and others filled with "a dark brown substance" responsible for the mottled appearance of achene.]

CORY, V. L. Six thistles introduced into Texas. Madroño **5:** 200–202. 1940. [First report of *Silybum Marianum* in Texas.]

FIEBIG, M., & H. WAGNER. Neue antihepatotoxisch wirksame Flavonolignane aus einer weissblühenden *Silybum*-Varietät. Pl. Med. **51:** 310–313. 1984.

FRANCO, J. DO AMARAL. *Silybum. In:* T. G. TUTIN *et al.*, eds., Fl. Europaea **4:** 126. 1976.

HAHN, G., H. D. LEHMANN, M. KÜRTEN, H. UEBEL, & G. VOGEL. Zur Pharmakologie und Toxikologie von Silymarin, des antihepatotoxischen Wirkprinzips aus *Silybum Marianum* (L.) Gaertner. Arzneim. Forsch. **18:** 698. 1968.*

HASSAN, N. M., F. M. HAMMOUDA, A. M. RIZK, H. RIMPLER, & S. I. ISMAIL. Isolation of silymarin from *Silybum Marianum* growing in Egypt. 33rd Annual Congress including the Business Section of the Society for Medicinal Plant Research, Regensburg, West Germany, Sept. 23–28. Acta Agron. Acad. Sci. Hung. **34**(Suppl.): 107. 1985.

HAWKES, R. B., L. A. ANDRES, & P. H. DUNN. Seed weevil released to control milk thistle. Calif. Agr. **26**(12): 14. 1972.* [*Rhinocyllus conicus.*]

HIKINO, H., Y. KISO, H. WAGNER, & M. FIEBIG. Antihepatotoxic actions of flavonolignans from *Silybum Marianum* fruits. Pl. Med. **50:** 248–250. 1984.

JOHNSON, M. F. Studies in the Virginia flora: species new to Virginia. (Abstr.) ASB Bull. **25:** 75. 1978. [*Silybum Marianum* in Goochland County, Virginia.]

KOUL, A. K., A. K. WAKHLU, & J. L. KARIHALOO. Chromosome numbers of some flowering plants of Jammu (Western Himalayas). II. Chromosome Inf. Serv. **20:** 32, 33. 1976.*

KOZLOWSKI, J., & M. HOLYNSKA. Effect of mineral fertilization on the crop yield of *Silybum Marianum* fruit and on the content and yield of silymarin. (In Polish.) Herba Polon. **31:** 51–60. 1986. [Rate of growth tied to both atmospheric conditions and to NPK (nitrogen, phosphorus, potassium) fertilization, which were found to be independent of each other.]

KUPICHA, F. K. *Silybum. In:* P. H. DAVIS, ed. Fl. Turkey **5:** 369. 1975.

LANGHAMMER, L. Anatomie und Histochemie der Früchte von *Silybum.* Pl. Med. **17:** 268–275. 1969. [Chemical composition of cell walls and storage substances in *S. Marianum.*]

LOTTER, H., & H. WAGNER. The stereochemistry of silybin (*Silybum Marianum*). Zeit. Naturforsch. C. Biosci. **38:** 339–341. 1983.*

MERICLI, A. H. *Silybum Marianum* in Turkey. Istanbul Univ. Eczacilik Fak. Mecm. **19:** 57–64. 1983.

POOK, E. W. The effect of shade on the growth of variegated thistle (*Silybum Marianum* L.) and cotton thistle (*Onopordum* sp.). Weed Res. **23:** 11–17. 1983.

SCHRALL, R., & H. BECKER. Callus und Suspensionskulturen von *Silybum Marianum.* II. Mitteilung: Umsetzung von Flavonoiden mit Coniferyalkol zu Flavonolignanen. (English abstr.) Pl. Med. **32:** 27–32. 1977. [Isolation of silybin from tissue culture.]

SHARMA, B. M., & P. SINGH. Pharmacognostic study of seeds of *Silybum Marianum.* Pl. Sci. Lucknow **6:** 34–37. 1974.

SINGH, J. P., B. K. KAPAHI, & Y. K. SARIN. Ecology of *Silybum Marianum* Gaertn. Jour. Econ. Taxon. Bot. **3:** 665–668. 1982.

SPITOVA, I. Germination dynamics and rate of germination of milk thistle (*Silybum Marianum* (L.) Gaertn.) seeds. UVTIZ (Ustav Vedeckotech Inf Zahradnictivi) Praha **11:** 322–329. 1984.

THIERET, J. W. Additions to the vascular flora of Louisiana. Proc. Louisiana Acad. Sci. **31:** 91–97. 1968. [*Silybum Marianum,* among others.]

WAGNER, H. Antihepatotoxic flavonoids. *In:* V. CODY, E. MIDDLETON, Jr., & J. B. HARBORNE, eds., Plant flavonoids in biology and medicine: biochemical, pharmacological and structure-activity relationships: proceedings. Buffalo, New York, July 2–26, 1985. New York. 1986.

———, O. SELIGMANN, L. HÖRHAMMER, M. SEITZ, & J. SONNENBICHLER. Zur Struktur von Silychristin, einem zweiten Silymarin-Isomeren aus *Silybum Marianum.* Tetrahedron Lett. **22:** 1895. 1971.

4. **Onopordum** Linnaeus, Sp. Pl. **2:** 827. 1753; Gen. Pl. ed. 5. 359. 1754.

Biennial herbs. Stems stout [very short], fistulose, much branched, spiny winged, densely tomentose, rarely glandular. Leaves near base of stem petiolate, middle to upper cauline leaves sessile, semi-auriculate, clasping; blades lanceolate to oblanceolate, toothed to pinnatifid [pinnatisect], glabrescent to arachnoid-tomentose; margins spiny. Capitula homogamous, discoid, terminal or axillary, solitary to corymbosely arranged, peduncles usually prickly winged.

Involucre hemispherical to globose [glabrescent or] arachnoid-tomentose; bracts imbricate in several series, narrowly lanceolate [oblanceolate], coriaceous, spine tipped, the margins scabrous; outer bracts commonly triangular, erect to recurved, adpressed to lax; inner bracts narrowly lanceolate, glabrescent. Receptacle flat to slightly convex, glabrous, fleshy, alveolate with short, basally fused scales along the margins of the pits, but never densely bristly. Flowers perfect, homogamous, actinomorphic to slightly zygomorphic. Corollas lilac to purplish, glabrous or with scattered sessile glands; tube slender, elongate, throat short, slightly expanded, actinomorphic or saccate and unequally divided by the sinuses of the linear, elongate lobes. Staminal filaments glabrous, attached at base of corolla throat; anthers sagittate, with narrow, acuminate, apical appendages often extending beyond corolla lobes. Style smooth or rugose below a distinct collar of hairs at base of the papillate, connate to slightly divergent branches. Achenes basifixed, 4–5 mm long, tetragonal, commonly laterally compressed, brown, rugulose, glabrous. Pappus bristles multiseriate, unequal, capillary or barbellate [plumose], often flattened, basally connate, deciduous as unit. Base chromosome number 17. LECTOTYPE SPECIES: *Onopordum Acanthium* L.; see Britton & Brown, Illus. Fl. No. U. S. Canada **3:** 556. 1913; also, Hitchcock & Green, Nom. Prop. Brit. Bot. 179. 1929; Jackson, Index Linn. Herb. 109. 1912. (Name Latinized from the ancient Greek name of the plant, *Onopordon*, from *onos*, donkey, and, *porde*, flatulence. Pliny stated that it caused flatulence in donkeys.)—SCOTCH THISTLE, COTTON THISTLE.

A genus of about 40 species of Mediterranean Europe and Western Asia. *Onopordum Acanthium* is naturalized in various parts of the world. *Onopordum* is distinguished from other thistles by the absence of bristles or paleae on the receptacle. The genus appears to be closely related to the large genus *Cousinia* Cass. and more remotely to *Jurinea* Cass. and *Saussurea* DC. *Onopordum Acanthium* is often found escaped from cultivation, established along roadsides, in dry, waste areas, and in disturbed pastures. It is the only species of this genus reported from the Southeast (Small, 1933; Cronquist, 1980), but it does not appear in the *Flora of the Carolinas* (Radford, *et al.*). McGregor reported *O. Acanthium* as a serious weed of infrequent, localized occurrence and often found in feedlots; Johnson (1974) noted only two collections from Virginia. Among *Onopordum* species, it can be distinguished by its large seeds and numerous slender, reflexed, involucral bracts (± 2 mm wide at the base).

Nearly 100 years have passed since the last revisionary treatment of the genus was published by Rouy, who recognized 24 species in three sections (*Acaulia* Rouy, *Erecta* Rouy, *Reflexa* Rouy) based on characters of habit, involucral bracts, and pappus. Rouy placed *Onopordum Acanthium* in sect. *Reflexa* (now ONOPORDUM), which was characterized by erect, winged stems, recurved involucral bracts, and scabrous or semi-plumose pappus bristles. Franco established the monotypic subgenus ACAULON and recognized four sections (ONOPORDUM, ERECTA, ECHINATA Franco, RECURVATA Franco) under subg. ONOPORDUM. The monotypic sect. ONOPORDUM was differentiated by its lanate or tomentose pubescence of unicellular hairs; lack of reticulate veins on the lower side of the leaves; linear-subulate, erecto-patent involucral bracts shorter than the flowers; eglandular corolla lobes; and scabrid pappus hairs.

A base chromosome number of 17 was indicated by Moore & Frankton's (1962) report of the chromosome number $2n = 34$ for *O. Acanthium* (see also Poddubnaja-Arnoldi and Morton, among others), *O. illyricum* L., and *O. Sibthorpianum* Boiss. & Heldr. All subsequent chromosome counts for species of *Onopordum* have been $2n = 34$ or $n = 17$ (see Moore, 1973; Goldblatt, 1981, 1984, 1985, for references). Moore & Frankton (1962) noted that the chromosome number and morphology of *Onopordum* are indistinguishable from those of *Cirsium.*

Relatively few phytochemical studies have been undertaken on *Onopordum.* The phenolic compound cynarin was reported from *O. illyricum,* and the alkaloids choline and stachydrine were reported from *O. Acanthium* (see Wagner for references). The sesquiterpene lactone onopordopicrin has been isolated from *O. Acanthium, O. leptolepis* DC., *O. tauricum* Willd., and two costunolide and melitensin sesquiterpene lactones were reported from *O. leptolepis* DC. (see Seaman for references). Rustaiyan *et al.* have isolated onopordopicrin and two related esters, eudesmanolides, and eudesmane derivatives from *O. carmanicum* (Bornm.) Bornm. Rustaiyan *et al.* reported that the 15-hydroxyl germacranolide with an 8-alpha-acyloxy group isolated from *O. carmanicum* is known from *Jurinea* (Hermout & Šorm) and that similar sesquiterpene lactones have been reported from *Centaurea, Arctium,* and *Cnicus* species, as well as from *Dicoma* Cass., of the Mutisieae.

REFERENCES:

Under tribal references see BOBROV & CZEREPANOV; BOISSIER; CRONQUIST, 1980; DITTRICH, 1970, 1977; FERNALD; GLEASON & CRONQUIST; GOLDBLATT, 1981, 1984, 1985; GOLTZ; HEGI, 1928–29, 1987; HERMOUT & ŠORM; HOWELL; JOHNSON, 1974; LAVIALLE; MABBERLEY; MCGREGOR; MOORE; MOORE & FRANKTON, 1962; MORTON; PODDUBNAJA-ARNOLDI; RICKETT; SEAMAN; SINGH & PANDEY; SMALL, 1933; WAGNER; and ZWÖFLER, 1965.

BOISSIER, E. *Onopordon.* Fl. Orient. **3:** 558–564. 1875.

CORY, V. L. Six thistles introduced into Texas. Madroño **5:** 200–202. 1940. [First report of *O. Acanthium* in Texas.]

DANIN, A. *Onopordum. In:* P. H. DAVIS, ed., Fl. Turkey **5:** 356–369. 1975.

DRESS, W. J. Notes on the cultivated Compositae 9: *Onopordum.* Baileya **14:** 75–86. 1966.

EIG, A. Revision of the *Onopordon* species of Palestine, Syria and adjacent countries. Palest. Jour. Bot. Jerusalem Ser. 2(4): 185–199. 1942.*

FORCELLA, F., & J. T. WOOD. Colonization potentials of alien weeds are related to their native distributions: Implications for plant quarantine. Jour. Austral. Inst. Agr. Sci. **50:** 35–41. 1984. [Comparative study of distributions of weedy species of *Carduus, Centaurea,* and *Onopordon* in Australia and in their native habitats.]

FRANCO, J. DO AMARAL. *Onopordum. In:* T. G. TUTIN *et al.,* eds., Fl. Europea **4:** 244–248. 1976.

GONZALEZ-COLLADO, I., F. A. MACIAS, G. M. MASSANET, J. M. OLIVA, F. L. RODRIGUEZ, & C. VERGARA. Chemical constituents of *Onopordum nervosum* Boiss. (In Spanish; English summary.) Ann. Quim. C. Quim. Org. Boiquim. **80:** 100, 101. 1984.*

MARTICORENA, C., & M. QUEZADA. *Onopordum Acanthium,* a new record of Compositae (Cynareae) in Chile. Bol. Soc. Biol. Concepción **51:** 301, 302. 1977.*

RECHINGER, K. H. *Onopordum. In:* K. H. RECHINGER, ed., Fl. Iran. **139a:** 156–164. 1979.

ROUY, G. Revision du genre *Onopordon.* Bull. Soc. Bot. France **43:** 577–599. 1896.

RUSTAIYAN, A., B. AHMADI, J. JAKUPOVIC, & F. BOHLMANN. Sesquiterpene lactones and eudesmane derivatives from *Onopordon carmanicum.* Phytochemistry **25:** 1659–1662. 1986.

5. **Arctium** Linnaeus, Sp. Pl. **2:** 816. 1753; Gen. Pl. ed. 5. 357. 1754.

Biennial herbs. Stems erect, striate, branching, glabrous to less often arachnoid-hairy; taproots stout, elongate. Leaves petiolate, petioles solid or fistulose; blades ovate to ovate-oblong, obtuse to cordate based, the upper surface with scattered sessile glands, the lower surface commonly arachnoid-hairy and glandular, the glands numerous, sessile; blade margins entire to serrate or rarely laciniate, often remotely dentate. Capitula homogamous, discoid, ca. 2–5 cm wide, borne in several- to many-headed racemes or cymes. Involucre subglobose, green [rarely purple], glabrous [or with arachnoid indumentum], bracts multiseriate, imbricate, narrowly lanceolate, subequal, coriaceous, basally appressed and slightly keeled, apices subulate, inwardly hooked, and on the outer bracts strongly reflexed. Receptacle flat, with numerous, white, subulate, scabrous scales. Flowers perfect, actinomorphic, corollas lavender to purple (rarely white), glabrous, tube narrow, equal to or slightly longer than the slightly expanded throat and acute to acuminate, elongate, glabrous lobes. Staminal filaments glabrous, anthers stramineous, sagittate, apical appendages with mucronate tips. Style slightly swollen at base, smooth below an indistinct collar of hairs found at the base of papillate, cuneate branches. Achenes basally attached, 4–7 mm long, oblong, somewhat compressed, apically truncate, commonly rugose, glabrous, many nerved, light to dark brown, often mottled. Pappus bristles numerous, unequal, relatively short (ca. 2 mm long), barbellate, individually and readily deciduous. LECTOTYPE SPECIES: *Arctium Lappa* L.; see Britton & Brown, Illus. Fl. No. U. S. Canada **3:** 547. 1913; also see Hitchcock & Green, Nom. Prop. Brit. Bot. 179. 1929. (Name from Greek, *arction,* a plant name from *arctos,* a bear, because of the rough involucre; cf. Munz.)—BURDOCK.

A Eurasian genus of about ten species, some of which are widely naturalized in southern Europe and Asia Minor, China(?), Japan, and North America. Three introduced species, *A. Lappa* L., great burdock; *A. minus* (Hill) Bernh., common burdock; and *A. tomentosum* Miller, woolly burdock, are known from the southeastern United States.

Perring recognized five species in Europe and, in the following quote, clearly stated the difficulties encountered in the taxonomy of the genus. "Specific limits within this genus cannot be clearly defined, each species showing great variation in hairiness of leaves and capitula, length of peduncles and colour of capitula and florets. All taxa are interfertile and although they are normally autogamous, outbreeding sometimes occurs. This has resulted in innumerable intermediates which are fully fertile and breed true from seed."

Four species (*Arctium Lappa, A. nemorosum* Lejeune & Courtois, *A. to-*

mentosum, and *A. minus*) based on characteristics of the achenes, corollas, involucral bracts, leaves and arrangement of the inflorescence were recognized by Fernald & Wiegand, but they were uncertain of the role hybridization had played among the taxa found in America. Arènes (1950) recognized four species (*A. Lappa, A. minus, A. tomentosum,* and *A. Chabertii*) and two sections, *Eglandulosa* (i.e., ARCTIUM including *A. Lappa* and *A. minus*) and GLANDULOSA. Each species was subdivided into various taxa. In addition, Arènes (1950) recognized nine interspecific hybrids involving *A. Lappa* or *A. minus,* two of which (*A.* ×*mixtum* Nym., *A.* ×*nothum* (Ruhm.) Weiss) were said to occur in North America (Moore & Frankton, 1974; Gross *et al.*). The division between glandular and eglandular taxa set forth by Arènes was considered to be a seemingly natural separation by Moore & Frankton. Cronquist (1980) notes that *A. nemorosum* may also be of hybrid origin.

The three species in the Southeast are found in waste places, along roadsides and streambanks, and in overgrazed pastures. As Gross *et al.* noted, the biennial habit of these species confines them to areas not cultivated or otherwise disturbed on an annual basis. Wiegand & Eames found that *A. minus* and *A. Lappa* are common in both rich soil and clay. Rollo *et al.* reported a strong overlap in distribution between *A. minus* and *A. Lappa* in their study area. All three are common in the Northeast, but only *A. minus* occurs with any regularity south of the Carolinas. Throughout its range in the Southeast it is more likely to be found in the mountains than in the Piedmont.

Mulligan & Kevan described *Arctium minus* as an autogamous biennial weed that is frequently visited by insects, despite the lack of any noticeable odor. These findings corroborated the work of Mulligan & Findlay, who noted that *A. minus* set viable seed even when covered with a "pollination bag." Gross & Werner reported that *A. minus,* which reproduces only by seed, will not flower in the second year if conditions are poor. Gross & Werner also determined that the probabilities of a rosette's flowering in a given year are linked to rosette size, but that rosette size is not linked to age. Total achene (hence seed) production was shown to be correlated with either rosette size or the height of the flowering stem, yet differences in total fruit production were shown to be a function of the number of capitula on a plant. No relationship was found between rosette size and the number of fruits in a capitulum (Gross & Werner).

Hawthorn & Hayne discovered that the mean number of fruits per plant in *A. minus* (13,400) was significantly greater than in *A. Lappa* (8200), as were the mean numbers of heads per plant (338 versus 112, respectively). Predispersal seed predation by the microlepidopteran *Metzneria lappella* accounted for the loss of 28 to 71 percent of the achenes of *A. minus* but only 15.5 percent of those of *A. Lappa.* Hawthorn & Hayne also found that only about one fifth of the heads of *A. minus* were shed during the winter compared to 62 percent of the heads of *A. Lappa.* This pattern of herbivory, along with the observation that very few achenes are dispersed from heads of *A. minus* because of the contraction of the involucre led Hawthorn & Hayne to conclude that *A. Lappa* is more efficient than *A. minus* in seed dispersal.

Rollo *et al.* observed four biotypes of *Arctium* present in their study populations. These biotypes, including the two parental species (*A. minus* and *A. Lappa*), were differentiated on the basis of size of capitula, length of peduncles, stem color, involucral characters, degree of insect herbivory, and allometric measurements. The relative abundance of these biotypes changed yearly. A "scenario" involving differential insect predation, hybrid inferiority, and differential dispersal was suggested to explain the dynamics of burdock populations. In accord with the study by Hawthorn & Hayne, Rollo *et al.* noted that the capitula of *A. minus* remain tightly closed allowing few achenes to fall out, while the capitula of *A. Lappa* open widely, allowing many achenes to fall beneath the parent plant. In addition, Rollo *et al.* observed that *A. minus* is more likely to colonize new, disturbed habitats than is *A. Lappa*, suggesting that this was due to the tightly closed capitula of *A. minus* that are not so readily deciduous as those of *A. Lappa*. They concluded that the capitula of *A. minus* are more suited to dispersal by animals to which they are readily attached by their hooked involucral bracts. Noting common burdock's extremely high seed mortality from the moth *Metzneria lappella*, Rollo *et al.* characterized *A. minus* as a fugitive species that depends on long-distance dispersal by animals to escape moth predation in both time and space.

On the basis of counts of $n = 18$ (Nakajima), $2n = 36$ (Tarnavschi) and $2n = 32$ (Sugiura) for *A. Lappa*; $2n = 36$ (Löve & Löve, 1944; Tarnavschi) for *A. nemorosum*; $2n = 36$ (Tarnavschi) and $2n = 32$ (Wulff) for *A. minus*; and $2n = 36$ for *A. tomentosum* (Poddubnaja-Arnoldi; Tarnavschi), Löve & Löve (1961) considered *Arctium* to have a basic chromosome number of nine. Mulligan has since reported $2n = 36$ for *A. minus*.

Despite many claims of hybridization between species of *Arctium* (Arènes, 1950; Moore & Frankton, 1974; Weigand & Eames), only one study has directly addressed this subject. Rollo *et al.* studied the allometric and electrophoretic variation between four biotypes representing two parental types (*A. minus, A. Lappa*) and two putative hybrids. They concluded that three of the four biotypes could be clearly distinguished by allometric measurements. Electrophoretic patterns showed unique isozymes in both parental biotypes which also differed from one another to the greatest extent allometrically. The putative hybrid biotypes were found to share various isozymes from the two parental types, thus supporting the hypothesis that these biotypes were hybrids.

The sesquiterpene lactone arctiopicrin was found in *Arctium minus, A. Lappa, A. nemorosum,* and *A. tomentosum* and onopordopicrin was isolated from *A. minus* (see Seaman for sources). In addition, the triterpenes β-eudesmol, arctiol, eremophilene petsitolone, and fucinanolide were reported for *A. Lappa* (see Wagner, 1977, for sources). Wagner (1977) reported the flavonoids isoquercitin, astragalin, quercetin 3-O-arabinoside, quercimeritrin, rutin, and kaempferol 3-O-rhamnoglucoside from *A. minus.* Alkaloids of unknown structure have also been reported for *A. Lappa* and three other unnamed species of *Arctium* (Wagner, 1977).

Some of the many economic uses of *Arctium* that have been well documented by Moore & Frankton (1974) include root extracts used as laxatives, diuretics, sudorifics, blood purifiers, and hair restorers, as well as constituents in "wood tea" and as an emergency coffee substitute (Hegi, 1929; Youngken, 1948).

Moore & Frankton also cited Rousseau & Raymond's report that the young leaves and dried roots were eaten by the American Indians until fairly recently, and Yanovsky's record that *A. Lappa* was eaten as greens and the roots were cooked for soup and dried and stored for winter food. *Arctium Lappa* is cultivated for its edible roots (*gobo*) in Japan, and the young leaves are used in salads in both Japan and Scandinavia (Mabberley). The hooked involucral bracts of *Arctium* were the inspiration for the now widely used "Velcro" fabric closures.

REFERENCES:

Under tribal references see CRONQUIST, 1980; DITTRICH, 1970, 1977; GAERTNER; GOLDBLATT, 1981, 1984, 1985; HEGI, 1928–29, 1987; JOHNSON, 1975; LAVIALLE; LESSING; LINNAEUS; LÖVE & LÖVE, 1944, 1961; MABBERLEY; MOORE & FRANKTON, 1974; PODDUBNAJA-ARNOLDI; RADFORD *et al.*; RICKETT; SEAMAN; SHISHKIN & BOBROV; SMALL, 1933; WAGNER, 1977; and WEIGAND & EAMES.

ARÈNES, J. Monographie du genre *Arctium* L. Bull. Jard. Bot. Bruxelles **20:** 67–156. 1950. [Four species in two sections (*A. Lappa* & *A. minus* in sect. *Eglandulosa*; *A. tomentosum* & *A. Chabertii* in sect. *Glandulosa*), all divided into various subspecific taxa.]

DE LANGHE, J. E. Les bardanes (genre *Arctium* L.) de Belgique et des régions voisines. Nat. Belges **47:** 21–29. 1966.

FERNALD, M. L., & K. M. WIEGAND. A synopsis of the species of *Arctium* in North America. Rhodora **12:** 43–47. 1910. [*A. Lappa, A. tomentosum, A. nemorosum,* and *A. minus*; representative specimens cited.]

GROSS, R. S., & P. A. WERNER. Probabilities of survival and reproduction relative to rosette size in the common burdock (*Arctium minus,* Compositae). Am. Midl. Nat. **109:** 184–193. 1983.

———, P. A. WERNER, & W. R. HAWTHORN. The biology of Canadian weeds 38. *Arctium minus* and *Arctium Lappa.* Canad. Jour. Pl. Sci. **60:** 621–634. 1980.

HAWTHORN, W. R., & P. D. HAYNE. Seed production and predispersal seed predation in the biennial Composite species, *Arctium minus* (Hill) Bernh. and *A. Lappa* L. Oecologia **34:** 285–295. 1978.

KUPICHA, F. K. *Arctium. In:* P. H. DAVIS, ed., Fl. Turkey **5:** 354–356. 1975.

MORITA, K., Y. NISHIJIMA, & J. KADA. Chemical nature of a desmutagenic factor from burdock (*Arctium Lappa*). Agr. Biol. Chem. **49:** 925–932. 1985.

MULLIGAN, G. A., & J. N. FINDLAY. Reproductive systems and colonization in Canadian weeds. Canad. Jour. Bot. **48:** 859–860. 1970.

——— & P. G. KEVAN. Color, brightness, and other floral characteristics attracting insects to the blossoms of some Canadian weeds. *Ibid.* **51:** 1939–1952. 1973.

NAKAJIMA, G. Chromosome numbers in some crops and wild angiosperms. Jap. Jour. Genet. **12:** 211–218. 1936. [*A. Lappa, n* = 18.]

NAYA, K., K. TSUJI, & U. HAKU. Constituents of *Arctium Lappa.* Chem. Lett. **3:** 235 ff. 1972.*

PARRISH, M. D., & J. M. BAIRD. Predispersal seed predation of common burdock (*Arctium minus*) by Abruchid coleoptera. Bull. New Jersey Acad. Sci. **27:** 26. 1982.

PERRING, F. H. *Arctium. In:* T. G. TUTIN *et al.,* eds., Fl. Europaea **4:** 215. 1976.

RECHINGER, K. H. *Arctium. In:* K. H. RECHINGER, ed., Fl. Iran. **139a:** 105–107. 1979.

REED, F. C., & S. N. STEPHENSON. Factors affecting seed number and size in burdock, *Arctium minus.* Proc. Michigan Acad. Sci. **5:** 449–455. 1973.*

ROBERTS, H. A., & J. E. NEILSON. Seed survival and periodicity of seedling emergence in 12 weedy species of Compositae. Ann. Appl. Biol. **97:** 325–334. 1981.

ROLLO, C. D., J. D. MACFARLANE, & B. S. SMITH. Electrophoretic and allometric variation in burdock (*Arctium* spp.); hybridization and its ecological implications. Canad. Jour. Bot. **63:** 1255–1261. 1985.

ROMINGER, J. M., J. M. RICKETSON, & W. HODGSON. Distribution of common burdock, *Arctium minus* Bernhardi (Compositae), in Arizona. Jour. Arizona Nevada Acad. Sci. **20:** 71. 1985.*

ROUSSEAU, J., & M. RAYMOND. Études ethnobotaniques québécoises. Contr. Inst. Bot. Univ. Montréal **55.** 1945.*

ROSTOVTSEVA, T. S. Chromosome numbers of some species of the family Asteraceae 2. Biol. Zhur. Leningrad **68:** 660–664. 1983. [*Arctium Lappa* L., $2n = 36$.]

SALEH, N. A. M., & B. A. BOHM. Flavonoids of *Arctium minus* (Compositae). Experimentia **27:** 1494. 1971.

SUGIURA, T. A list of chromosome numbers in angiospermous plants. Bot. Mag. Tokyo **45:** 353–355. 1931.

———. Studies on the chromosome numbers in higher plants, with special references to cytokinesis. I. Cytologia **7:** 544–595. 1936.

TARNAVSCHI, I. T. Die Chromosomenzahlen der Anthophyton-Flora von Rumänien mit einem Ausblick auf das Polyploidie-Problem. Bull. Jard. Mus. Bot. Univ. Cluj **28**(Suppl.):1–130. 1948.

WASHINO, T., M. YOSHIKURA, & S. OBATA. New sulfur containing acetylenic compounds from *Arctium Lappa.* Agr. Biol. Chem. Tokyo **50:** 263–269. 1985.*

WULFF, H. D. Chromosomenstudien an der schleswig-holsteinischen Angiospermenflora. I. Ber. Deutsch. Bot. Ges. **55:** 262–269. 1937.*

YANOVSKY, E. Food plants of the North American Indians. U. S. Dep. Agr. Misc. Publ. **237.** 84 pp. 1936.*

YOUNGKEN, H. W. A textbook of pharmacognosy. Ed. 6. 1063 pp. Philadelphia. 1948.

Subtribe CENTAUREINAE Dumortier, Fl. Belg. Prodr. 72. 1827.

6. **Centaurea** Linnaeus, Sp. Pl. **2:** 909. 1753; Gen. Pl. ed. 5. 389. 1754.

Annual to perennial herbs [rarely dwarf shrubs with spiny branches or larger evergreen shrubs]. Stems tomentose or scabrous to hirsute with multicellular hairs, rarely glabrous, commonly with sessile glands. Leaves sessile to (less often) petiolate, alternate or all basal; blades narrowly lanceolate to ovate, entire to pinnatifid; margins scarcely or not at all prickly. Capitula heterogamous, discoid or falsely radiate, hemispherical to subglobose, terminal or axillary, commonly solitary or in loose cymose clusters, subsessile to long pedunculate. Involucre ovoid, subglobose [nearly cylindrical, oblong or fusiform], commonly contracted apically, bracts imbricate in several series, often striate, glabrous to tomentose, either shortly spine tipped or more commonly with an orbicular, lanceolate or triangular, scarious or hyaline, erose to pectinate appendage, or occasionally the appendage absent and the apical margin merely pectinate or lacerate. Receptacle flat to slightly convex, with numerous smooth, white bristles. Florets perfect or sterile. Corollas lavender, blue, yellow, or white; marginal florets sterile [perfect], occasionally with an irregularly expanded, falsely radiate corolla; inner florets perfect, discoid, actinomorphic, tube often elongate, slender, throat expanded, lobes long, linear to lanceolate. Staminal filaments glabrous; anthers stramineous or commonly the same color as corolla, tailed at base, though often shortly, the apical appendage narrow, acute. Styles smooth below a distinct collar of hairs at base of the short, slightly divergent, narrowly truncate to acute, papillate branches. Achenes obliquely or laterally attached to receptacle, oblong or ovoid, compressed or obtusely 4-angled, seldom evidently nerved, glabrous at maturity. Pappus of several series of unequal scabrous or barbellate [plumose] bristles or narrow scales, often much reduced, or absent. LECTOTYPE SPECIES: *Centaurea Centaurium* L.; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. **3:** 556. 1913; also, R. McVaugh, Fl. Novo-Galiciana, 209. 1982. (Name from Greek, of the centaurs, who were said to have used it in healing.)—KNAPWEED, STAR-THISTLE.

A genus first proposed by Linnaeus for 50 species, *Centaurea* currently is comprised of some 450 (Mabberley) to 600 species (Holub, 1972a; Wagenitz, 1985a). Various members of this genus have become widespread throughout the world, but species diversity is concentrated in the Mediterranean and Near Eastern regions. Dostál (1976) included 221 species in his treatment of *Centaurea* for the *Flora Europaea,* and Wagenitz recognized 172 in the *Flora of Turkey* (1975) and 89 in *Flora Iranica* (1980). Wagenitz (1985a) indicated that 260 species in 38 sections are known from Southwest Asia, with the greatest numbers in southern and eastern Turkey and adjacent Iran and Iraq. In this area, there are several widespread species, as well as 201 endemics, many of which occupy restricted areas. The large number of endemics and the coherent distribution of most groups (often delimited as subgenera, sections or, in some cases, genera) led Wagenitz (1985a) to conclude that speciation has occurred in relatively recent times and *in situ.* Further, Wagenitz believed that the diversity of the group can only be understood by taking into account the capitulum which, according to both Wagenitz and Burtt, functions as a single flower and its fruit might in other families. To illustrate this point, Wagenitz noted the wide range in the number of flowers per capitulum in different species (4 or 5 in *C. virgata* Lam. to over 200 in *C. macrocephala* (Muss.) Puschk. ex Willd.), as well as several forms of dispersal: a well-developed pappus as a means of wind dispersal (anemochory); small, deciduous capitula with hooked appendages suited for animal dispersal of whole capitula (epizoochory); and an elaisome that mediates dispersal by ants (myrmecochory). (See also Dittrich, 1968a, b.)

Only two species are indigenous in the United States: *Centaurea americana* Nutt., which enters the Southeast in western and southwestern Arkansas (E. B. Smith, 1988) and western Louisiana, and *C. Rothrockii* Greenman, a species of the Great Plains. However, nearly twenty other species have become established in parts of the United States, some as pernicious weeds.

Species of *Centaurea* in the southeastern United States are most often found in disturbed fields, waste places, and along roadsides. Cronquist (1980) recognized eight species in the Southeast, but several taxa (*C. dubia* Suter., *C. nigra* L., *C. Jacea* L., *C. Calcitrapa* L.) that he treated occur, if at all, only sporadically along the northern boundaries of this region. Three of these species (*C. dubia, C. Jacea, C. nigra*) are perennials that are widespread in the Northeast. They are distinguished from other taxa of *Centaurea* in the Southeast and from each other by leaf characters and subtle distinctions of the involucral bract appendages (Cronquist, 1980, among others).

The dubious occurrence of various taxa is reflected in Johnson's inclusion (see distribution maps in Harvill *et al.*) of *C. Calcitrapa, C. dubia, C. nigrescens* Willd., and *C.* ×*pratensis* Thuill. (*C. Jacea* × *C. nigra*), which are not treated by Ahles in Radford *et al.* Small (1933) considered only *C. solstitialis* L., *C. melitensis* L., and *C. Calcitrapa* to be naturalized and *C. Cyanus* L. to have escaped from cultivation in the Southeast.

Centaurea Cyanus, bachelor's-button or cornflower, is a widely cultivated winter annual that is periodically found to be well established in fields and waste places and along roads. It is distinguished by its narrow, nearly linear leaves and heads with an outer series of elongate, zygomorphic flowers, the corollas of which are usually bright blue (or occasionally pink or white).

Centaurea maculosa Lam., spotted knapweed, a short-lived perennial that has become one of the most serious weeds of western rangelands (Boggs & Story), is commonly encountered in old fields and pastures and along roadsides in the Southeast. Although similar to *C. Cyanus* in having an outer series of elongate, expanded florets, *C. maculosa* differs in its pinnatifid leaves and lavender flowers.

As noted by Cronquist (1980), *C. melitensis,* a yellow-flowered European species similar in many respects to *C. solstitialis* (also yellow flowered), is found only occasionally in South Carolina and Georgia. *Centaurea solstitialis,* a widespread and pernicious weed in several western states, is not well established in the Southeast. *Centaurea Calcitrapa,* another uncommon introduction to this region, can be differentiated from *C. solstitialis* by its purple florets, wingless stems, and epappose achenes. Both of these species are readily differentiated from others of *Centaurea* by their strongly spiny involucral bracts.

Centaurea americana, an annual plant common in grasslands in the Great Plains and most readily distinguished by its large, unarmed heads and well-developed pappus, enters the Southeast along the eastern border of its range which extends from Missouri southward through western Arkansas and the border of Louisiana with Texas, as noted above.

From the time of Cassini to the present, the question of generic boundaries in the subtribe Centaureinae and related subgeneric groupings within *Centaurea sensu lato* has generated considerable controversy. The rather lengthy account that follows outlines a part of the difficulty and complexity of the group.

Early in his serial publications on the Compositae in the *Dictionnaire des Sciences Naturelles,* Cassini (1817) recognized the tribes Cardueae (as "Carduacées") and Centaureeae (as "Centauriées"), both names invalidly published, to which he attributed 17 and 11 genera, respectively. Later (1819), he validated these and other tribes with Latin names. By 1830, when he completed his treatment for publication, Cassini had come to recognize in the Centaureeae 41 genera, nearly 30 of which he described himself. He aligned the Centaureeae with the Cardueae and Carlineae, but considered the possibility of recognizing the Cardueae and Centaureeae as subtribes of a single tribe, Cardueae. Initially, Cassini had differentiated Centaureeae from Cardueae by characteristics of the anther appendages (apically fused and curved, not straight as in the Cardueae), achene, and pappus. He noted that while both the Centaureeae and Cardueae have laterally compressed, obovate achenes with four more or less pronounced sides or ribs, the basal areole ("l'aréole basilaire") or point of attachment of the achene of the Cardueae is sessile, broad ("large"), smooth ("plane"), curved ("arrondie"), slightly oblique ("un peu oblique-antérieure"), and lacking a rim or margin. The Centaureeae, on the other hand, were reported to have sessile, very oblique basal areoles strongly adherent to the receptacle ("la substance du clinanthe") and situated in a broad, diamond-shaped notch with curvilinear sides ("une large échancrure en losange, à bords curvilignes").

As Cassini observed, the pappus of the Centaureeae is considered to be double or two ranked. The outer rank is comprised of several series of imbricate squamellae, the outermost of which are extremely short, flattened, obtuse, and barbellate. There is a gradual transition from the outer squamellae to an inner series of longer, cylindrical, bristle-like setae. A single series of very short, membranaceous, truncate squamellae constitutes the innermost rank of the double pappus. The pappus of the Cardueae is comprised of numerous series of unequal barbellate setae; the outermost series is composed of very short, filiform bristles, while the inner series is of barbellate setae flattened at the base, triangular ("triquètres") in the mid part, and filiform near the apex. In later descriptions, Cassini (1830) noted the outwardly curved corollas and outer series of sterile flowers in the Centaureeae (absent in the Cardueae) and the unique zygomorphic nature of the corollas in the Cardueae as differentiating characters. These distinctions, which have been the foundation for many subsequent classifications, were used by Dittrich (1977).

Lessing placed in synonymy under *Centaurea* nearly 30 genera that Cassini had described. Until recently, Lessing's concept of the tribe and of *Centaurea* has been followed by most workers.

Spach's tribal arrangement, patterned on Cassini's, included many of the characters Cassini used to delimit the tribes. Spach's proposed classification of *Centaurea* included 27 subgenera, six of which (*Chartolepis* Cass., *Jacea* Miller, *Cyanus* (Miller) Pers., *Lopholoma* Cass., *Hymenocentron* Cass., *Calcitrapa* (Heist ex Fabr.) Pers.) he treated in detail. Although he utilized suites of characters from the flowering capitula in his descriptions, differences in the involucral bracts were stressed in his segregation of these six taxa.

Bentham followed Lessing's tribal treatment in many respects but returned the Arctoteae and Calenduleae to tribal status. The subtribe Centaureinae comprised ten genera in Bentham's treatment. *Centaurea* was divided into 22 series ("vix Sectiones") most of which were based on Cassini's genera.

The first infrageneric treatment for *Centaurea* was put forth by A. P. de Candolle in the third edition of Lamarck & De Candolle's *Flore Française* (1805). Six sections were proposed by De Candolle (see Brizicky) as reductions of Jussieu's generic concepts: *Centaurea* (involucral bracts entire, foliaceous, not spinose), *Rhaponticum* (Ludwig) DC. (involucral scales scarious, not ciliate or spinose), *Cyanus* (Miller) DC. (involucral scales ciliate, not spinose), *Seridia* (Juss.) DC. (involucral scales terminated with numerous prickles disposed like fingers of the hand), *Calcitrapa* (Heist. ex Fabr.) DC. (involucral scales terminated by one spine that is laterally divided towards the base), and *Crocodylium* (Hill) DC. (involucral scales terminated by a simple spine).

Shortly afterward, Persoon (1807) proposed ten subgenera for *Centaurea*

(*Amberboa* Pers., *Phrygia* Pers., *Cyanus* (Miller) Pers., *Jacea* (Miller) Pers., *Stoebe* (L.) Pers., *Calcitrapa* (Heist. ex Fabr.) Pers., *Seridia* (Juss.) Pers., *Crocodylium* (Hill) Pers., *Verutum* Pers., and *Crupina* Pers.) based primarily on involucral bract characters similar to those used by De Candolle in his sectional treatment.

In the year that Cassini finished his series of articles for Cuvier's *Dictionnaire des Sciences Naturelles,* George Don (1830) put forth a classification with six sections, including five of those proposed by De Candolle (*Centaurea, Cyanus, Calcitrapa, Seridia, Crocodylium*). Don described the section *Crupina* (involucral scales entire), as well as subsections for most of the other sections included in his treatment.

De Candolle's treatment in his *Prodromus* (1837) divided *Centaurea* into five series and 31 sections. Article 33.4 of the International Code of Botanical Nomenclature rules that De Candolle's sections and series were invalidly published because of their inverted order (i.e., sections as subdivisions of series). As with his earlier sectional treatment (see above), De Candolle relied on characters of the involucre to differentiate his series, but expanded his delimitation of sections to include characteristics of the involucre, flowers, achenes, and pappus. The majority of the sections recognized by De Candolle were originally described by Cassini as genera.

De Candolle's inclusive treatment was followed by many subsequent workers, including Bentham (see above) and Hoffmann. Utilizing characters of the involucre and pappus, Hoffmann recognized in *Centaurea* 41 sections, many of which were based on Cassini's genera. Several of De Candolle's sections were treated as genera by Boissier (e.g., *Aetheopappus* Cass., *Psephellus* Cass., *Phaeopappus* (DC.) Boiss.), who also recognized as genera groups treated as infrageneric categories by other workers (e.g., *Stizolophus* Cass., *Acroptilon* Cass., *Melanoloma* Cass.). Boissier distinguished 16 sections in *Centaurea.*

Hayek's (1901) classification comprised nine subgenera (*Centaurium, Microlophus* (DC.) Hayek, *Calcitrapa, Cyanus, Jacea, Odontolophus* (Cass.) Hayek, *Crocodylium, Cheirolophus* (Cass.) Hayek, *Plectocephalus* Hayek) and 18 sections (mostly in the subgenera *Calcitrapa, Cyanus,* and *Jacea*) in a well-documented treatment of *Centaurea* in Austria-Hungary. Hayek proposed five new sections (*Eucalcitrapa* (subg. *Calcitrapa*), *Eucyanus* and *Pannophyllum* (subg. *Cyanus*), *Eujacea* (subg. *Jacea*), *Eucheirolophus* (subg. *Cheirolophus*)) differentiated, for the most part, by characteristics of the involucral bract appendages.[4]

More recently, still other systems have been presented in anatomical, palynological, cytological, and floristic studies. Wagenitz's (1955) work on the pollen morphology and systematics of *Centaurea* has been used by subsequent workers as a basis for various systematic schemes (e.g., Dostál, 1973; Dittrich, 1977; Guinochet; Guinochet & Foissac). Wagenitz recognized eight pollen types (*Serratula, Centaurium, Crupina, Scabiosa, Dealbata, Jacea, Montana, Cyanus*) in *Centaurea sensu lato* based on differences in size and shape of the grains and the sculpturing and structure of the exine. His data came from about 26

---

[4] The use of the prefix "Eu-" is specifically ruled against in Article 21.3 of the International Code.

sections of *Centaurea* and from 16 closely related genera. Wagenitz's observations have been elaborated on by Štepa (1959, 1960) and Velari. Velari noted, in confirmation of Wagenitz, that *Centaurea* presented solitary, isopolar and radiosymmetric pollen grains, the shape of which varied from suboblate to euprolate. In addition, the grains were reported to be tricolporate with operculate apertures, and the sculpturing was described as echinate, echinulate, or verrucate.

Dittrich (1968a, b) studied in considerable detail the morphology and anatomy of achenes from eleven genera and in *Centaurea* from nearly 25 sections. He concluded that the form of the hilum (basal, lateral, or caudate), the mechanisms for fruit detachment (the elaiosomes or simple parenchymatic tissues), achene pubescence, and the consistency of the pericarp are important for the determination of generic boundaries in the Centaureinae. While considerable variation can be noted in pappus characters of taxa in the Centaureinae, Dittrich proposed a new definition of single and double pappus in this group and concluded that this character is of limited value for defining genera in this subtribe.

Dittrich (1977) recognized 27 genera in the subtribe Centaureinae. In a manner very similar to that of Cassini, he characterized the group by the concave and lateral-adaxial orientation of the detachment area of their fruits and their "double pappus" comprised of an outer rank of bristles or scales elongated from outside to inside and an internal rank often different from the outer.

Utilizing Wagenitz's (1955) seven basic pollen types as the groundwork for his "inner taxonomy," Dostál (1973) resurrected numerous old generic names, elevated several sections of *Centaurea* to generic rank and described a new genus, *Wagenitzia* Dostál. This resulted in the recognition of approximately 50 segregates from *Centaurea sensu lato.* Combinations in several of the genera recognized by Dostál were made by both Holub (1972b) (*Acosta* Adanson, *Colymbada* Hill emend. Holub, *Cyanus* Miller, *Jacea* Miller) and Sojak (*Cyanus, Jacea, Calcitrapa* Heister ex Fabr., *Xanthopsis* (DC.) Koch, *Heterolophus* Cass., *Acosta*; lectotypes were provided for *Behen* Hill, *Psora* Hill, and *Sagmen* Hill). The lack of detailed knowledge of the western Asiatic and Mediterranean groups led Dostál (1975) to reconsider making the numerous nomenclatural combinations necessary if these segregates are recognized as genera as he had earlier proposed (Dostál, 1973). Instead, his account for the *Flora Europaea* (Dostál, 1976) treated *Centaurea* as comprising 12 subgenera and 26 sections.[5]

Jeffrey (1968) listed 59 genera of the Centaureeae from the most "Mutisioid"

---

[5] The combination subgenus *Microlophus* (Cass.) Dostál appears to be based on a rejection of the earlier combination subgenus *Microlophus* (DC.) Hayek. The rejection of Hayek's name appears to be due to Hayek's use of De Candolle's illegitimate sectional name (section *Microlophus* (Cass.) DC.) (see Article 33.4 in the International Code of Botanical Nomenclature; also see discussion above referring to De Candolle's series and sectional treatment). Dostál's combination should be rejected as a later homonym (Article 64.1 of the Code), whether or not one regards De Candolle's sectional names to have been invalidly published. Contemporary authors (Dostál, 1976; Wagenitz, 1955, 1975, 1980) have tacitly, if not explicitly, rejected De Candolle's series nomenclature by their acceptance of his sectional nomenclature.

genera to those that he considered most specialized. Jeffrey's list begins with *Warionia* Benth. & Coss., a genus assigned to the Mutisieae by Dittrich. The next nine taxa listed by Jeffrey were placed by Dittrich (1977) in the tribe Carlineae, and these were followed by *Echinops* and *Acantholepis* Less., of the tribe Echinopseae. The remaining taxa of Jeffrey's list were assigned to the tribe Cardueae by Dittrich, but Jeffrey's list intermixed taxa placed in the subtribes Centaureinae and Carduinae by Dittrich (1977). Jeffrey did not intend to indicate acceptance of taxa at the generic level by their inclusion in his list, except for the 11 genera (*Centaurea, Cirsium, Cnicus, Cyanus, Cynara, Echinops, Goniocaulon, Plectocephalus, Rhaponticum, Silybum, Volutaria*) included in his key to genera of East Tropical Africa. Jeffrey included *Cnicus, Goniocaulon, Plectocephalus,* and *Rhaponticum* in his key, even though they had not been recorded for this area. A more extensive key was presented by Jeffrey for 17 genera that he considered worthy of recognition apart from *Centaurea* on the basis of differences in filament and style-branch pubescence, characters Jeffrey found to correlate well with the pollen types established by Wagenitz (1955). He further noted that subgenus CENTAUREA is a small group more distinct from other members of *Centaurea sensu lato* than many groups that have been segregated as genera by earlier workers. For a consistent treatment, Jeffrey held that *Centaurea* would have to be restricted to subg. CENTAUREA. If such a system were adopted, however, Jeffrey believed that the numerous nomenclatural recombinations that would have to be made would result in a "clearly undesirable" situation. Jeffrey recognized nine subgenera of *Centaurea* based on filament and achene pubescence and the pollen types of Wagenitz.

The eight species of *Centaurea* (*C. americana, C. Calcitrapa, C. Cyanus, C. dubia, C. Jacea, C. maculosa, C. nigra, C. solstitialis*) found in the Southeast have, as noticed above, been placed in different subgeneric categories and, in some cases, different genera by European workers. *Centaurea americana* is the type species of *Plectocephalus* D. Don (Dostál, 1973), but within *Centaurea* it has been placed in sect. *Plectocephalus* (D. Don) DC. (Wagenitz, 1955; Dittrich, 1968a). Dostál (1976) incorrectly synonymized *C. dubia* under the later name *C. transalpina* Schleicher ex DC., a species that he included in subgenus *Jacea* sect. *Nigrescentes* (Hayek) Dostál. Hayek (1901), however, treated *C. transalpina* as a synonym of *C. dubia* in (subgenus *Jacea*) sect. *Eujacea* Hayek.

Centaurea Jacea, the type species of *Jacea* Miller (Dostál, 1973), and *C. nigra* were both placed in sect. *Jacea* (Miller) DC. (Wagenitz 1955, 1975; Dittrich, 1968a) and in subg. *Jacea* (Miller) Hayek (Clapham *et al.*). Dostál (1976) retained *C. Jacea* in subg. *Jacea,* sect. *Jacea,* but placed *C. nigra* in sect. *Lepteranthus* (DC.) Dumort. Since these two species frequently hybridize (see below), certain workers (Briquet, 1931; Wiegand & Eames) have considered them to be conspecific.

Centaurea Cyanus ($2n = 24$; Löve & Löve, 1961, as *Cyanus arvensis* Moench), the type species of *Cyanus* Miller (Dostál, 1973), was placed in subgen. *Odontolophus* (Cass.) Hayek by Dostál (1976) and in sect. *Cyanus* (Miller) DC. by Wagenitz (1975).

Centaurea maculosa ($2n = 18, 36$; Löve & Löve, 1961, as *Acrolophus maculosus* (Lam.) Cass.) has been placed variously in the genus *Acosta* Adanson

(Holub, 1972b), subg. *Acrolophus* sect. *Maculosae* (Hayek) Dostál (Dostál, 1976), and sect. *Acrolophus* (Cass.) DC. (Wagenitz, 1955; Hayek, 1901), while *C. Calcitrapa* ($2n = 20$; Löve & Löve, 1961, as *Calcitrapa stellata* Lam.), the type species of *Calcitrapa* Heister ex Fabr. (Dostál, 1973), has been placed in sect. *Calcitrapa* (Wagenitz, 1955, 1975) and subg. *Calcitrapa* (Dostál, 1976).

Centaurea solstitialis ($2n = 16$) has been placed in the genus *Leucantha* S. F. Gray (Löve & Löve, 1961), subg. *Solstitiaria* (Hill) Dobrocz. (Dostál, 1976; Clapham *et al.*), and sect. *Mesocentron* (Cass.) DC. (Wagenitz, 1955).

The only comprehensive treatment of *Centaurea* for the United States and adjacent Canada is that by Moore (1972), who treated 28 species. Within his key to species, taxa were grouped according to sectional characteristics. Moore & Frankton (1954) put forth cytological and morphological justification for segregating *C. repens* L., a widespread weed of the Western States, as *Acroptilon repens* (L.) DC. (see also Dostál, 1973).

Sectional classification based on pollen data (Wagenitz, 1955) was considered to be congruent with classifications based on involucral characters and chromosome number by Guinochet, who tentatively proposed that groups with high base chromosome numbers, nearly entire involucral bracts, relatively complex pollen structure (*Serratula* type), generally large capitula, large, entire leaves, and perennial habit gave rise to groups with lower chromosome numbers, complex involucral bracts, relatively simple pollen structure (*Jacea* type), normally small capitula, often deeply divided leaves, and annual or biennial habit.

Guinochet postulated base chromosome numbers of 8, 9, 10, 11, 12, 13, and 15 for *Centaurea*. His study of the karyotypes showed a correspondence between the size and the number of chromosomes. Guinochet hypothesized that the lower chromosome base numbers evolved from the higher ones by way of translocations and loss of chromosomes. These chromosomal mutations were considered by him to have played a primary role in the differentiation of species, subspecies, and varieties, and further that polyploidy had affected speciation in only a secondary manner.

Hypotheses of hybridization and introgression have been used to explain plants morphologically intermediate between taxa otherwise considered distinct (Arènes, 1948, 1949, 1957; Chiapella; Georgiadis; Marsden-Jones & Turrill; Roy). Other studies (Ockendon *et al.*; Elkington & Middlefell) have found little or no evidence of hybridization and claim that certain *Centaurea* species (e.g., *C. nigra* L.) are highly variable. In particular, the taxa included in sect. JACEA (including *C. Jacea, C. nigra, C. dubia,* and *C. nigrescens* of the Southeastern species) have been studied extensively, and the number of species recognized in this group has fluctuated from one (Briquet, 1902, 1931) or a few variable species (Guinochet) to as many as seven distinct ones (Arènes, 1957; Marsden-Jones & Turrill). All the species of this section have chromosome numbers of $2n = 22$ or $2n = 44$ (Guinochet; Guinochet & Foissac; Roy; Löve & Löve, 1961; Gervais; Moore, 1968; Marsden-Jones & Turrill).

Extensive and well-documented crossing experiments (Marsden-Jones & Turrill) indicate that *C. nigra* and *C. Jacea* produce fertile offspring when selfed and will, in general, breed true for characters of the involucre and flower color.

Hybrids between *C. Jacea* and *C. nigra* were readily evident, and backcrossing between hybrid offspring and the parental lines produced a wide range of flower and involucral characteristics. In some cases, interspecific crossing seemed to lead to abnormalities in the formation of the androecium. Marsden-Jones & Turrill reported that in some extensive hybrid swarms, pure forms of *C. Jacea* have disappeared.

The distribution of sesquiterpene lactones has been used in attempts to clarify taxonomic boundaries within both *Centaurea* and the subtribe Centaureinae (Geppert *et al.*; Nowak *et al.*; see above under tribal discussion), but no classification based on phytochemistry has been proposed to date. The numerous sesquiterpene lactones known from *Centaurea* have been reviewed by several authors (Wagner, Seaman, Nowak *et al.*, Geppert *et al.*) and will not be reiterated here.

Compounds isolated from species known from the Southeast include cynaropicrin from *C. americana* (Ohno *et al.*), cnicin from *C. Calcitrapa* (Jakupovic *et al.*), scabiolide from *C. Calcitrapa* and *C. solstitialis,* and chlorohyssopifolin A from *C. nigra* and *C. solstitialis.* (See Seaman for citations and sesquiterpenes known from *Centaurea* up to 1982.)

A wide variety of flavonoids, including three flavones (centaurein, jacein, jaccoside) from *C. Jacea* and two (swertisin, isoswertisin) from *C. Cyanus* (see Wagner for citations and structural components), has been reported from *Centaurea.*

Stevens (1982) and Stevens & Merrill reviewed the wide range of biological activity (cytotoxicity, phytotoxicity, actinioplasticity, and allergenicity, among others) attributed to sesquiterpene lactones and suggested that these compounds may play a role in the allelopathy attributed to *C. repens* and *C. solstitialis.* They concluded that these compounds affect root growth in a similar, yet more pronounced, manner to auxins, but do not affect seed germination.

REFERENCES:

Under tribal references see BENTHAM, 1873a & b; BOBROV & CZEREPANOV; BOISSIER; BOLICK; BOULTER *et al.*; BRIQUET, 1931; BRIZICKY; BURTT; CASSINI; CLAPHAM *et al.*; CRONQUIST, 1980; DITTRICH, 1968a, 1968b, 1977; DON, 1830; HEGI, 1928–29, 1987; HOFFMANN; JEFFREY, 1968; LAMARCK & DE CANDOLLE, LESSING; LÖVE & LÖVE; PERSOON; SEAMAN; E. B. SMITH; SPACH; ŠTEPA, 1959, 1960; WAGNER, 1977; WIEGAND & EAMES; ZOHARY; ZWÖFLER, 1965, 1978.

APPENDINO, G., P. GARIBOLDI, & F. BELLIARDO. Sesquiterpene lactones from *Centaurea uniflora* subsp. *nervosa.* Phytochemistry **25:** 2163–2165. 1986.

ARÈNES, J. Les *Centaurea* hybrides de l'Herbier du Muséum d'Histoire Naturelle. Bull. Soc. Fr. Éch. Pl. Vasc. **2:** 27–30. 1948; **3:** 34, 35. 1949.

———. Le groupe spécifique du *Centaurea paniculata* L. sensu latissimo. Mém. Mus. Hist. Nat. Paris Bot. **2:** 175–266. 1951. [Subgen. *Acrolophus.*]

———. Les Centaurées de la sous-section *Jacea.* Systématique, chorologie et phylogénie. Bull. Jard. Bot. Bruxelles **27:** 143–157. 1957.

———. Sur les Centaurées de la sous-section *Phrygiae* Boiss. Not. Syst. Paris **15:** 376–390. 1959. [Five species and a number of subspecific taxa keyed and described, and their phylogeny discussed; putative hybrids between these and other species listed.]

ARMITAGE, A. M. Spotlight on centaureas. Am. Nurseryman. Pp. 60–65. January, 1988.

Blanca Lopez, G. Revisión del género *Centaurea* L. sect. *Willkommia* G. Blanca. Lagascalia **10**: 131–205. 1981.

Blaringhem, L. Études sur le polymorphisme floral. 11. Variabilité, sexualité et fécondité du *Centaurea pratensis* Thuill. Bull. Soc. Bot. France **67:** 311–318. 1920. [*C. pratensis* treated as a distinct species (in contrast to Gadeceau's earlier treatment) with considerable variation in flower, pollen, and achene morphology, as well as variation in the distribution of flower types in the capitula.]

Boggs, K. W., & J. M. Story. The population age structure of spotted knapweed (*Centaurea maculosa*) in Montana. Weed Sci. **35:** 194–198. 1987.

Bohlmann, F., & R. K. Gupta. Guaianolides from *Centaurea canariensis.* Phytochemistry **20:** 2773, 2774. 1981.

Briquet, J. Monographie des Centaurées des Alpes Maritimes. Bâle et Genève. 1902.*

Britton, C. E. Note on *Centaurea.* Jour. Bot. **57:** 340–342. 1919.

Carlstrom, A. New taxa and notes from the SE Aegean area and SE Turkey. Willdenowia **15:** 73–78. 1986.

Chiapella, L. F. Biosistematica di alcune centauree della sezione *Acrocentron* Cass. Giorn. Bot. Ital. **113:** 237–252. 1979.

Chicoine, T. K., & P. K. Fay. The longevity of viability of spotted knapweed seeds in Montana soils. Proc. West. Soc. Weed Sci. **37:** 204–207. 1984.* [*C. maculosa.*]

Cory, V. L. Six thistles introduced into Texas. Madroño **5:** 200–202. 1940. [*Centaurea melitensis, C. Picris.*]

Cusma Velari, T. Scanning electron microscopic studies of *Centaurea* L. s.s. pollen. Giorn. Bot. Ital. **116:** 201–210. 1984.

——— & A. Vuerich. Pollen and systematic morphology in *Centaurea* section *Eujacea.* Meeting of the Societa Botanica Italiana Congresso Sociale (Social Congress of the Italian Botanical Society), Prato, Italy, Oct. 12–14. Giorn. Bot. Ital. **116**(Suppl. 1.): 76, 77. 1982.*

Czerepanov, S. Commentationes de systematica *Centaureinarum.* I, II. (In Russian.) Not. Syst. Leningrad **19:** 442–457. 1959; **20:** 457–489. 1960.

Dobrochayeva, D. M., & I. M. Kotov. Taxonomy of the genus *Centaurea* L. s.l. (English summary.) Ukrayin. Bot. Zhur. **19:** 39–44. 1962. [Includes new species.]

Dormer, K. J. The taxonomic significance of crystal forms in *Centaurea.* New Phytol. **61:** 32–35. 1962. [Calcium oxalate found in parenchyma of ovary walls reported in two mutually exclusive forms: prismatic and curvilinear crystals. Prismatic crystals found in 81 of 112 species. This character was shown not congruent with Wagenitz's (1955) classification based on pollen morphology.]

Dostál, J. Étude préliminaire de l'évolution et de la systématique des types du genre *Centaurea* sect. *Cyanus* subsect. *Montanae.* Preslia **10:** 57–69. 1931.

———. Taxonomick-studie o celedích Lycopodiaceae a Asteraceae a o rodech *Lycopodium* a *Centaurea.* Acta Univ. Palackianae Olomucensis, Fac. Rer. Nat. **31:** 5–40. 1969.*

———. Preliminary notes on the subtribe Centaureinae. Acta Bot. Acad. Sci. Hung. **19:** 73–79. 1973.

———. New nomenclatural combinations and taxa of the Compositae subtribe Centaureinae in Europe. *In:* V. H. Heywood, ed., Fl. Europaea. Notulae systematicae ad floram Europaeam spectantes. No. 18. Bot. Jour. Linn. Soc. **71:** 191–210. 1975.

———. *Centaurea. In:* T. G. Tutin *et al.,* eds., Fl. Europaea **5:** 254–301. 1976.

Drozdz, B., & J. Piotrowski. Lactones of *Carduinae* subtribe. Pol. Jour. Pharmacol. Pharm. **25:** 91–94. 1973.*

Earle, F. R., I. A. Wolff, & Q. Jones. Search for new industrial oils. III. Oils from the Compositae. Jour. Am. Oil Chem. Soc. **37:** 254–256. 1960. [*Centaurea Cyanus* reported to have high concentrations of dienoic acids suitable for applications dependent on reactions of linoleic acid.]

ELKINGTON, T. T., & L. C. MIDDLEFELL. Populational variation within *Centaurea nigra* L. in the Sheffield region. Watsonia **9:** 109–116. 1972.

FELDMAN, L. J., & E. G. CUTTER. Regulation of leaf form in *Centaurea solstitialis* L. I. Leaf development of whole plants in sterile culture. Bot. Gaz. **131:** 31–39. 1970. II. The development potentialities of excised leaf primordia in sterile culture. *Ibid.* 39–49. [Heteroblastic leaf development regulated in part by endogenous levels of gibberellins. Suggested that in transition to flowering levels of endogenous gibberellins rise, resulting in production of small, entire leaves below capitula, whereas lower levels of gibberellins had brought about production of deeply lobed leaves on lower portions of stem. Plants grown on media with high concentrations of gibberellic acid produce only entire, unlobed leaves, while plants grown on media with a gibberellic acid inhibitor produce lobed leaves.]

FERNANDEZ CASAS, J. Númericos cromosómicos de plantas españolas, III. Lagascalia **6:** 91–96. 1977. [*C. antennata*, $2n = 22$; *C. Haenseleri*, $2n = 44$.]

FLETCHER, R. A., & A. J. RENNEY. A growth inhibitor found in *Centaurea* spp. Canad. Jour. Pl. Sci. **43:** 475–481. 1963.

GADECEAU, E. Observations critiques sur le groupe de *Centaurea Jacea* L. Bull. Soc. Bot. France **67:** 55–63. 1920. [Discussion of taxa closely related to *C. Jacea*, including *C. nigra* and *C. pratensis* as varieties.]

GARDOU, C. Sur la signification de la pectination des appendices des écailles chez *Centaurea Jacea* L. s.l. Bull. Soc. Bot. France **112:** 153–163. 1965.

———. Analyse du mode de reproduction chez *Centaurea Jacea* L. *sensu lato*. Compt. Rend. Acad. Sci. Paris, Sci. Nat. **265:** 912–914. 1967.*

———. Sur quelques tentatives d'hybridization expérimentale intraspecifique chez *Centaurea Jacea* L. s.l. *Ibid.* 1195–1198.*

———. Caryosystématique des Centaurées de la section *Acrocentron* Cass. Bull. Soc. Bot. France **116:** 29–38. 1969.

———. Recherches biosystématiques sur la section *Jacea* Cass. et quelques sections voisins du genre *Centaurea* L. en France et dans les régions limitrophes. Feddes Repert. **83:** 311–472. 1972.

GEORGIADIS, T. Problèmes de différenciation et d'introgression dans *Centaurea* subg. *Acrolophus* Compositae en Grèce. Bot. Jahrb. Syst. **102:** 321–337. 1981.

———. Pollen de *Centaurea* en Grèce. (English summary.) Pollen Spores **27:** 29–51. 1985. [Differentiation in pollen morphology associated with geographical orientation and cytological characters; a relation between pollen and floral morphology noted.]

GEPPERT, B., B. DROZDZ, M. KEILCZEWSKI, & M. HOLUB. Sesquiterpene lactones XXIII. Isolation of sesquiterpene lactones from *Centaurea* L. species. Acta Soc. Bot. Polon. **52:** 23–34. 1983. [18 taxa analyzed; lactones reported were salonitonolide, cnicin, cynaropicrin, acroptillin, repin, and janerin. Study did not involve species that occur in the southeastern U. S.]

GERVAIS, C. Annotated list of chromosome numbers of the northeastern American vascular flora. Nat. Canad. **106:** 451–462. 1979.

GILLOT, X. Sur la gynodioecie de la *Centaurea Jacea* L. Ann. Soc. Bot. Lyon **21:** 67–69. 1896.

GONZALEZ, A. G., J. BERMEJO, & G. M. MASSANET. Aportación al estudio quimiotaxonomico del genero *Centaurea*. Rev. Latinoamer. Quim. **8:** 176–181. 1977.

———, J. BERMEJO-BARRERA, T. ZARGOZA-GARCIA, & F. ESTEVEZ-ROSAS. Sesquiterpene lactones from *Centaurea* species. Phytochemistry **23:** 2071, 2072. 1984.

GUGLER, W. Die Centaureen des ungarischen National-Museums. Ann. Hist. Nat. Mus. Hung. **6:** 15–297. 1907.

GUINOCHET, M. Contribution a l'étude caryologique du genre *Centaurea* L. sens. lat. Bull. Soc. Hist. Nat. Afr. Nord. **48:** 282–300. 1957. [*C. ruthenica* Lam., $n = 15$.]

——— & J. FOISSAC. Sur les caryotypes de quelques espèces du genre *Centaurea* L. et leur signification taxonomique. Rev. Cytol. Biol. Veg. **25:** 373–389. 1962.

GUYLAS, S., & J. PESTI. Data on the anatomy of nectaries of *Centaurea* species. Acta Biol. Szeged. **12:** 17–24. 1966.

HARVILL, A. M., JR., T. R. BRADLEY, & C. E. STEVENS. Atlas of the Virginia flora. Part II. Dicotyledons. 147 pp. Farmville, Virginia. 1981.

HAYEK, A. VON. Die *Centaurea*-Arten Österreich-Ungarns. Denkschr. Acad. Wiss. Wien, Math.-Nat. **70:** 585–773. 1901.

———. Prodromus florae peninsulae Balcanicae. Fedde Repert. Spec. Nov. Beih. 30. **2:** 735–795. 1931. [*C. nigra, C. Jacea, C. dubia, C. solstitialis, C. maculosa* treated as separate species; *C. dubia* Suter. with three subspecific divisions corresponding to *C. nigrescens* Willd., *C. vochinensis* Bernh., and *C. smolinensis* Hayek.]

HESLOP-HARRISON, Y., & K. R. SHIVANNA. The receptive surface of the angiosperm stigma. Ann. Bot. II. **41:** 1233–1258. 1977. [*Centaurea* said to have dry, papillate stigmas.]

HOLUB, J. On correct generic names of *Acrocentron* Cass. and *Acrolophus* Cass. (*Centaurea* L. s.l.). Preslia **44:** 215–218. 1972a.

———. New nomenclatural combinations in *Centaureinae.* Acta Bot. Acad. Sci. Hung. **19:** 73–79. 1972b.

———. Brief comments on the 4th volume of *Flora Europaea.* Preslia **49:** 311–327. 1977.

HULL, E. D. *Centaurea maculosa* in Indiana. Rhodora **48:** 391. 1946.

JAKUPOVIC, J., Y. JIA, V. P. PATHAK, F. BOHLMANN, & R. M. KING. Bisabolone derivatives and sesquiterpene lactones from *Centaurea* species. Pl. Med. **5:** 399–401. 1986.

JONES, G. N. *Centaurea maculosa* in Illinois. Rhodora **49:** 84. 1947.

KAMANZI, K., J. RAYNAUD, & B. VOIRIN. Flavonoid C-glucosyls from the flowers of *Centaurea melitensis* L. (Compositae). Pl. Med. Phytother. **17:** 47–51. 1983.

LACK, A. J. Competition for pollinators in the ecology of *Centaurea Scabiosa* and *Centaurea nigra.* I. Variation in flowering time. New Phytol. **91:** 297–308. 1982a. II. Observations on nectar production. *Ibid.* 309–320. 1982b. III. Insect visits and the number of successful pollinations. *Ibid.* 321–339. 1982c.

LOPEZ, G. B. Notas cariosistemáticas en el género *Centaurea* section *Wilkommia* G. Blanca. II. Conclusiones. Anal. Jard. Bot. Madrid **38:** 109–126. 1981.

MADDOX, D. M., A. MAYFIELD, & N. H. PORITZ. Distribution of yellow starthistle (*Centaurea solstitialis*) and Russian knapweed (*Centaurea repens*). Weed Sci. **33:** 315–327. 1985. [Light infestations (<450 ha.) of *C. solstitialis* reported Davidson County, Tennessee, and Halifax County, N. Carolina. None of *C. repens* reported for states of the southeastern U. S., but heavy infestations reported in large areas of Virginia.]

MARSDEN-JONES, E. M., & W. B. TURRILL. British knapweeds. 201 pp. Dorking, England. Printed for the Society of London. 1954. [A thorough treatment with many valuable notes, particularly on subg. *Jacea.*]

MASSIOT, G., A. M. MORFAUX, L. LE MEN OLIVIER, J. BOUQUANT, A. MADACI, A. MAHAMOUD, M. CHOPOVA, & P. ACLINOU. Guaianolides from the leaves of *Centaurea incana.* Phytochemistry **25:** 258–261. 1986.

MCGREGOR, R. L. *Centaurea.* Pp. 898–901 *in* Great Plains Flora Association, Flora of the Great Plains. Lawrence, Kansas. 1986.

MERRILL, G. B., & K. L. STEVENS. Sesquiterpene lactones from *Centaurea solstitialis.* Phytochemistry **24:** 2013–2018. 1985.

MOORE, R. J. *In* A. LÖVE, IOPB Chromosome number reports. XVIII. Taxon **17:** 419–422. 1968.

———. Distribution of native and introduced knapweeds (*Centaurea*) in Canada and the United States. Rhodora **74:** 331–346. 1972.

——— & C. FRANKTON. Cytotaxonomy of three species of *Centaurea* adventive in Canada. Canad. Jour. Bot. **32:** 182–186. 1954. [Support segregation of *C. repens* as

Acroptilon Cass.; distinguishing characters: all flowers perfect and similar; achenes smooth, slenderly obovoid; scar basal, not oblique; pappus 9 mm long, caducous; hyaline margin of "tegules" (phyllaries) entire; $n = 13$, unknown in other sections of *Centaurea*.]

NILSSON, A. The flora along the railways in the Landskona area southernmost Sweden. Svensk. Bot. Tidskr. **78:** 293–307. 1984.

OCKENDON, D. J., S. M. WALTERS, & T. P. WHIFFEN. Variation within *Centaurea nigra* L. Proc. Bot. Soc. Brit. Is. **7:** 549–552. 1969.

OHNO, N., H. HIRAI, H. YOSHIOKA, X. A. DOMINGUEZ, & T. J. MABRY. Cynaropicrin, a sesquiterpene lactone from *Centaurea americana*. Phytochemistry **12:** 221, 222. 1973.

OKSUZ, S., & H. AYYILDIZ. Sesquiterpene lactones from *Centaurea coronopifolia*. Phytochemistry **25:** 535–537. 1986.

———, ———, & C. JOHANSSON. 6-Methoxylated and C-glycosyl flavonoids from *Centaurea* species. Jour. Nat. Prod. **47:** 902, 903. 1984.

PAVLETIC, Z. A study of taxonomical relations between the species *Centaurea rupestris* and *Centaurea Fritschii* and their spontaneous hybrid *Centaurea sordida*. (Asteraceae-section *Acrocentron*). Acta Bot. Croat. **42:** 137–144. 1983.

PHILIPSON, B. A. An enumeration of the tropical African species of *Centaurea*. Jour. Bot. **77:** 227–234. 1939. [Provides a key to 22 species.]

PRODAN, J. Centaureele Romaniei (Centaureae Romaniae), Monographie. (Subgen. *Cyanus*). (In Hungarian & German.) Bul. Acad. Inolte Studii Agron. Cluj Mem. **1.** 256 pp., *63 pls.* 1930.* [Monograph of *Centaurea* in Romania.]

ROCHE, B. F., JR., G. L. PIPER, & C. J. TALBOTT. Knapweeds of Washington. Exten. Bull. Wash. State Univ. Coop. Exten. Serv. **1393.** 41 pp. Nov. 1986.*

RÖSLER, H., A. E. STAR, & T. J. MABRY. New 6-Methoxyflavonols from *Centaurea Jacea*. Phytochemistry **10:** 450, 451. 1971.

ROY, B. Chromosome numbers in some species and hybrids of *Centaurea*. Jour. Genet. **35:** 89–93. 1937.

SAARISALO-TAUBERT, A. A study of hybridization in *Centaurea* section *Jacea* in eastern Fennoscandia. Ann. Bot. Fenn. **3:** 86–95. 1966.*

SINGH, R. P., & A. K. PANDEY. Development and structure of seeds and fruits in Compositae-Cynareae. Phytomorphology **34:** 1–10. 1984.

SOJÁK, J. Nomenklatorické poznámky (Phanerogamae). Cas. Nár. Mus., Odd. Prír. **140:** 127–134. 1972.

SOSNOVSKY, D. I. Über zwei Sektion der Gattung *Centaurea* L. s.str. (In Russian; German summary.) Monit. Jard. Bot. Tiflis. II. **5:** 21–34. 1931.*

SPACH, E. Histoire naturelle des végétaux. **10:** 10–15, 65–72. 1841. Paris. [Source of several subgeneric names in *Centaurea*.]

STEFANOV, B., & T. GEORGIEV. Beitrag zur Begrenzung der Arten der Gattung *Centaurea* L. von der Sekt. *Cyanus* DC. Spis. Balg. Akad. Nauk. **44:** 133–193. 1931.*

STEVENS, K. L. Sesquiterpene lactones from *Centaurea repens*. Phytochemistry **21:** 462, 463. 1982.

———. Allelopathic polyacetylenes from *Centaurea repens* (Russian knapweed). Jour. Chem. Ecol. **12:** 1205–1211. 1986.

——— & G. B. MERRILL. Sesquiterpene lactones and allelochemicals from *Centaurea* species. Pp. 83–98 *in* ACS. Symp. Ser. Am. Chem. Soc. 268. 1985. [Based on "Symposium on the chemistry of allelopathy, biochemical interactions among plants," April 1984, St. Louis, Missouri.]

——— & R. Y. WONG. Structure of chlororepdiolide, a new sesquiterpene lactone from *Centaurea repens*. Jour. Nat. Prod. **49:** 833–837. 1986.

SULYOK, G., & A. LASLO-BENCSIK. Cyanidin 3-(6-succinyl glucoside)-5-glucoside from flowers of seven *Centaurea* species. Phytochemistry **24:** 1121, 1122. 1985.

TAKEDA, K., & S. TOMINAGA. The anthocyanin in blue flowers of *Centaurea Cyanus*. Bot. Mag. Tokyo **96:** 359–363. 1983.

TAMAS, M., & S. STOLERIU. Chromatographic identification of anthocyanidins and anthocyanosides in some flowers and fruits of indigenous plants. Stud. Cercet. Biochim. **19**(1): 113–120. 1976.*

TAMURA, H., T. KONDO, Y. KATO, & T. GOTO. Structures of a succinyl anthocyanin and a malonyl flavone. Two constituents of the complex blue pigment of cornflower, *Centaurea Cyanus*. Tetrahedron Lett. **24**: 5749–5752. 1983.*

TSANKOVA, E., & I. OGNYANOV. New sesquiterpene lactones from *Centaurea phrygia*. Pl. Med. **5**: 465, 466. 1985.

TZVELEV, N. Notulae criticae de sectionibus nonnullis generis *Centaureae* L. (In Russian.) Not. Syst. Leningrad **19**: 409–441. 1959.

UPADHYAYA, M. K. Induction of bolting by gibberellic acid in rosettes of diffuse (*Centaurea diffusa*) and spotted (*Centaurea maculosa*) knapweed. Canad. Jour. Bot. **64**: 2428–2432. 1986. [Bolting induced by gibberellic acid, a significant correlation between rosette age and gibberellic acid treatment noted; gibberellic acid did not induce bolting in plants less than 40 days old.]

VALDÉS-BERMEJO, E., & M. P. A. MATA. Estúdios cariológicos en especies ibéricas del género *Centaurea* L. (Compositae). I. Anales Jardin Bot. Madrid **40**: 119–142. 1983.

VAN LOON, J. C., & H. DE JONG. *In:* IOPB chromosome number reports LIX. Taxon **27**: 53–61. 1978. [*Centaurea diffusa*, $2n = 36$; *C. maculosa* ssp. *maculosa*, $2n = 18$.]

WAGENITZ, G. Pollenmorphologie und Systematik der Gattung *Centaurea* L. s.l. Flora **142**: 213–279. 1955. [The definitive study on which many subsequent classifications have been based.]

———. Über einige Arten der Gattung *Centaurea* aus der Türkei. Willdenowia **2**: 456–468. 1960a.

———. *Centaurea* L. sect. *Cynaropsis*, eine neue Sektion der Gattung aus Vorderasien. *Ibid.* 469–494. 1960b.

———. Die Eingleiderung der Phaeopappus-Arten in das System von *Centaurea*. Bot. Jahrb. **82**: 137–215. 1963.

———. *Centaurea*. *In:* Materials for a Fl. Turkey XXX: Compositae, I. (Compiled by P. H. DAVIS.) Notes Bot. Gard. Edinburgh **33**: 217–231. 1974.

———. Parallele Evolution von Merkmalen in der Gattung *Centaurea*. Phyton Austria **16**: 301–312. 1975.

———. *Centaurea*. *In:* P. H. DAVIS, ed., Fl. Turkey **5**: 465–585. 1975.

———. *Centaurea*. *In:* K. H. RECHINGER, ed., Fl. Iran. **139b**: 313–420. 1980.

———. *Centaurea* and the Index Kewensis. Taxon **32**: 107–109. 1983. [Of the 2070 entries examined by the author, nearly 25 percent (488) were found to be incorrect citations; in addition, "a considerable number" of names were reported by the author to have been omitted from the Index.]

———. The flora of Arabia 7. *Centaurea* in the Arabian Peninsula. Notes Bot. Gard. Edinburgh **41**: 457–466. 1984.

———. A new species of *Centaurea* (Compositae) from Iraq. Kew Bull. **40**: 793, 794. 1985.

———. *Centaurea* in Southwest Asia: patterns of distribution and diversity. Second symposium on plant life of Southwest Asia, Edinburgh, Scotland, September 16–20, 1985. Proc. Roy. Soc. Edinburgh B. Biol. Sci. **89**: 11–22. 1986.

——— & E. GAMAL-ELDIN. Zur Kenntnis der griechischen *Centaurea*-Arten der Sektion *Acrocentron*. (English summary.) Bot. Jahrb. **107**: 95–127. 1985. [Revision of the 25 species of section *Acrocentron* known from Greece.]

7. **Cnicus** Linnaeus, Sp. Pl. **2**: 826. 1753; Gen. Pl. ed. 5. 358. 1754, nom. cons.

Erect annual herbs, the stems branching, arachnoid-villous. Leaves of the lower stem commonly short-petiolate, upper leaves sessile; blades lanceolate, up to 20 cm × 5 cm, subcoriaceous, sinuate-dentate or pinnatifid, scarcely or not at all decurrent, lower surface conspicuously veined and densely glandular, margins weakly spiny or ciliate. Capitula heterogamous, discoid, solitary at the end of branches, closely subtended by ovate or lanceolate cauline leaves. Involucre campanulate to ovoid, often obscured by cauline leaves; bracts imbricate, multiseriate, ovate-lanceolate, the outer mucronate-subulate, the inner longer, with a pectinate to spine-like apical appendage. Receptacle flat; scales numerous, setaceous. Outer flowers inconspicuous, sterile, with a very slender 2- or 3-lobed corolla; inner flowers perfect, their corollas slightly zygomorphic, yellow, glabrous or minutely glandular, with the tube narrow, elongate, ca. 8–10 mm long, the throat expanded, slightly saccate, unequally divided by the sinuses of the lanceolate, glabrous corolla lobes with two sinuses considerably deeper than the other three. Staminal filaments pubescent, connected at base of throat; anthers stramineous with a firm, narrow, apical appendage, shortly saggitate tailed at base. Style smooth below a distinct collar of hairs at base of the short, scarcely divergent, papillate branches. Achenes obliquely attached to receptacle, ca. 8 mm long, subterete, strongly 20 ribbed, glabrous, with a firm 10-toothed crown. Pappus biseriate, the outer of 10 long, minutely scabrid, stramineous awns, alternating with 10, much shorter, white, minutely hairy and sparsely pectinate inner bristles. (*Carbenia* Adanson.) TYPE SPECIES: *C. benedictus* L., typ. cons. (See Hitchcock & Green, Nomencl. Prop. Brit. Bot. 179. 1929, for discussion.) (A Latin name of the safflower (*Carthamus* L.), from Greek *cnecos.*)—BLESSED THISTLE.

A single species of the Mediterranean region widely naturalized in many parts of the Northern Hemisphere.

Cronquist (1980) characterized *Cnicus benedictus* in the Southeast as sparingly established in fields and waste places. This species is found scattered throughout the Piedmont and along the Coastal Plain from Virginia, south through Georgia and Alabama, but apparently it neither extends as far west as Texas (Correll & Johnston), nor is it found in the Great Plains flora (Barkley, 1986).

Linnaeus included five species in his treatment of *Cnicus.* Adanson recognized the genus *Carbenia* for two species, one of which was *C. benedictus.* Apparently unaware of Adanson's *Carbenia,* Gaertner redefined *Cnicus* as a monotypic genus based on the unique pappus characters of *C. benedictus.* Persoon incorporated *Cnicus* as a subgenus of *Carduus,* but treated *Cnicus benedictus* as a member of *Centaurea* subgenus *Calcitrapa.* While Don recognized *Cirsium* and placed therein many taxa treated by earlier authors under *Cnicus,* he, too, treated *C. benedictus* under *Centaurea* (sect. *Calcitrapa*). Lessing's recognition of *Cnicus* for *C. benedictus* was followed by De Candolle, who provided an extensive list of excluded species. Both Lessing and De Candolle placed *Cnicus* in the subtribe Centaureinae. Bentham recognized *Carbenia* Adans. for *Cnicus benedictus* and broadly circumscribed *Cnicus* to include many taxa currently placed in *Cirsium.* Neither Hoffmann nor Spach followed Bentham but treated *Cnicus* as it was delineated by Gaertner. Asa Gray (1884a, b, 1874), on the other hand, did follow Bentham's circumscription (see discussion under *Cirsium*) and included *Cnicus benedictus* in *Centaurea.* Such nomenclatural confusion led to the conservation of *Cnicus* L. emend. Gaertner in 1935 (Hitchcock & Green). Contrary to most floristic treatments of the past fifty years, Ahles in Radford *et al.* placed *Cnicus* in synonymy under *Centaurea* from which it is readily distinguished by its pappus structure and fruit characters (Dittrich, 1970).

Chromosome numbers reported for *Cnicus benedictus* are $2n = 20$ and $2n = 17$ (see Mehra *et al.*; Goldblatt, 1981, for references).

Medicinal qualities have been attributed to *Cnicus* (Franco) particularly for the glucoside cnicin for its antimicrobial and antibiotic activity (Wagner; Schneider & Lachner; Vanhaelen-Fastré) and for treatment for gout (Mabberley). In addition to cnicin, another sesquiterpene lactone, salonitenolide, and monoterpenes have been isolated from *C. benedictus* (Seaman).

REFERENCES:

Under tribal references see ADANSON; BARKLEY, 1986; BENTHAM, 1873a; BOBROV & CZEREPANOV; DE CANDOLLE; CORRELL & JOHNSTON; CRONQUIST, 1980; DON; GAERTNER; GOLDBLATT, 1981; GRAY, 1874, 1884a, b; HEGI, 1928–29, 1987; HOFFMANN; LESSING; MEHRA *et al.*; MORTON; MUNZ; PERSOON; RADFORD *et al.*; SEAMAN; SPACH; and WAGNER.

ARYVAND, A. *In:* IOPB chromosome reports LVIII. Taxon **26:** 557–565. 1977.

FRANCO, J. DO AMARAL. *Cnicus. In:* T. G. TUTIN *et al.*, eds., Fl. Europaea **4:** 301, 302. 1976.

KORTE, F., & G. BECKMANN. Über die Bitterstoffe aus *Cnicus benedictus.* Naturwissenschaften **45:** 390. 1958.

KUPICHA, F. K. *Cnicus. In:* P. H. DAVIS, ed., Fl. Turkey **5:** 588–590. 1975.

RECHINGER, K. H. *Cnicus. In:* K. H. RECHINGER, ed., Fl. Iran **139b:** 428–430. 1980.

SCHNEIDER, G., & I. LACHNER. Beitrag zur Analytik und Wirkung von Cnicin. Pl. Med. **53:** 247–251. 1987.

VANHAELEN-FASTRÉ, R. Antibiotic and cytotoxic activities of cnicin, isolated from *Cnicus benedictus.* Jour. Pharm. Belg. **27:** 683. 1972.*